

Upper Albian and Lower Cenomanian ammonites from the Mfamosing Quarry, Calabar Flank, Cross River State, south-eastern Nigeria

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16 Text-Figures, 1 Table, 6 Plates

Ammonites Albian Cenomanian Mfamosing Limestone Calabar Flank Cross River State Nigeria

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Abstract

The Upper Albian and Lower Cenomanian ammonites from the abandoned Mfamosing Limestone Quarry of the Calabar Cement Company (Calcemco) in Cross River State, south-eastern Nigeria, are described. The highly fossiliferous, ferruginous, pyritic and in part nodular phosphatic mineralized hardground at the top of the Mfamosing Formation at this classic locality has yielded a diverse fauna. The index species of the upper Upper Albian *Pervinquieria (Subschloenbachia) rostrata* Zone, and the succeeding *P. (S.) perinflata* Zone occur as large limestone moulds. A diverse predominantly phosphatised or pyritic Lower Cenomanian fauna is correlated with the widely recognized lower *Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone, with *Puzosia (Anapuzosia)* sp., *Stoliczkaia (Lamnayella) juigneti* (WRIGHT & KENNEDY, 1978), *Salaziceras nigerianum* FÖRSTER & SCHOLZ, 1979, *Flickia bullata* sp. nov., *Graysonites wacoense* (BÖSE, 1928), *Utaturiceras* sp., *Acompsoceras calabarense* ZABORSKI, 1985, *Acompsoceras* sp. juv., *Mariella (M.) bicarinata* (KNER, 1852), *Mariella (M.) essenensis* (GEINITZ, 1849), *Mariella (M.) oehlerti oehlerti* (PERVINQUIÈRE, 1910), *Mariella (M.)* aff. *miliaris* (PICTET & CAMPICHE, 1861), *Mariella (M.) cenomanensis* (SCHLÜTER, 1876), and *Hypoturrilites betaitraensis* COLLIGNON, 1964.

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Eine Ammonitenfauna des späten Albiums und frühen Cenomaniums aus dem Mfamosing Steinbruch, Calabar Flank, Cross River State, Südostnigeria

Zusammenfassung

Aus dem fossilreichen Hardground am Top der klassischen Lokalität der Mfamosing-Formation im inzwischen stillgelegten Mfamosing-Kalkstein-Steinbruch der Calabar Cement Company (Calcemco) wird eine diverse, stratigrafisch kondensierte Ammonitenfauna beschrieben. Die Fauna weist sowohl die namensgebende Art der *Pervinquieria (Subschloenbachia) rostrata*-Zone des obersten Albiums auf, als auch der darüber folgenden *P. (S.) perinflata*-Zone. Sie kann mit der weithin anerkannten *Neostlingoceras carcitanense*-Subzone der *Mantelliceras mantelli*-Zone des unteren Cenomaniums korreliert werden. Aus letzterer konnten folgende Taxa nachgewiesen werden: *Puzosia (Anapuzosia*) sp., *Stoliczkaia (Lamnayella) juigneti (*WRIGHT & KENNEDY, 1978), *Salaziceras nigerianum* FÖRSTER & SCHOLZ, 1979, *Flickia bullata* sp. nov., *Graysonites wacoense* (BÖSE, 1928), *Utaturiceras* sp., *Acompsoceras calabarense* ZABORSKI, 1985, *Acompsoceras* sp. juv., *Mariella (M.) bicarinata* (KNER, 1852), *Mariella (M.) essenensis* (GEINITZ, 1849), *Mariella (M.) oehlerti oehlerti* (PERVINQUIÈRE, 1910), *Mariella (M.)* aff. *miliaris* (PICTET & CAMPICHE, 1861), *Mariella (M.) cenomanensis* (SCHLÜTER, 1876) und *Hypoturrilites betaitraensis* COLLIGNON, 1964.

Introduction

Unless otherwise stated, the fossils described in this paper were collected in 1976 and 1977 by Lobitzer at the now abandoned Mfamosing limestone quarry of the Calabar Cement Company (Calcemco). The quarry is located close to Mfamosing village on the "Calabar Flank" at latitude 5°04'16'' north, longitude 8°32'20'' east, some 33 km north-east of Calabar, the capital of Cross River State in south-eastern Nigeria (Text-Fig. 1). The Calabar Flank is situated on the southern slopes of the Precambrian crystalline basement complex of the Oban Massif. It constitutes the southernmost part of the Benue Trough, which extends across Nigeria from the south-west to the northeast.

Most of the samples were collected in situ on the bedding plane of the intraformational hardground on top of the Mfamosing Limestone, while some represent loose specimens, collected either on the in situ weathered hardground or from scree after blasting.

Previous research

The limestone potential of south-eastern Nigeria was already recognised in early studies by the Geological Survey of Nigeria (e.g. RAEBURN, 1937; TATTAM, 1939; ORAJA-KA, 1959a, b), who also published the geological mapsheet 80 Oban Hills in the scale 1:250,000 (GEOLOGICAL SURVEY OF NIGERIA, 1957). In addition to the economic evaluation of the limestone and marl occurrences, REYMENT (1952, 1955, 1965, 1972, 1980) initiated biostratigraphic investigations on ammonite-bearing localities in the region. Later, Reyment continued this work partly in the frame of IGCP-project 58 "Mid Cretaceous Events" (e.g. REYMENT & DINGLE, 1987; REYMENT & MÖRNER, 1977; REYMENT & TAIT, 1983). Reyment was also the first to examine, albeit briefly, the ammonites described below. The late Reinhard Förster (Munich) contacted Lobitzer and published two papers based on the ammonite-fauna described in detail here, as well as additional material he had collected (FÖRSTER, 1978; FÖRSTER & SCHOLZ, 1979). These contributions already recognized the condensed Upper Albian-Lower Cenomanian character of the hardground faunas on top of the Mfamosing Limestone. The geology of the Calabar Flank also attracted prominent local geoscientists, who contributed essential papers and added greatly to our knowledge of this spectacular region (e.g. ADEGOKE et al., 1976; EKWUEME et al., 1995; ESSIEN & UFOT, 2010; FAY-

OSE & DESSAUVAGIE, 1976; FAYOSE, 1978; PETTERS, 1982; PETTERS & REIJERS, 1987; KOGBE, 1989; NAIR et al., 1982; NYONG, 1995; NYONG & RAMANATHAN, 1985; UMEJI, 2013).

Since the researches of Lobitzer in Nigeria in the years 1976 and 1977, many papers have been published, in particular on the sedimentology, diagenesis and stratigraphy of the Mfamosing Limestone and the overlying Eze-Aku Shale Formation. The main focus of the present paper is the ammonite fauna of the hardground on top of the Mfamosing Limestone. Accordingly, the manyfold studies outside the context of the present paper, as the subdivision of the Asu River Group by various authors, is not discussed here.

According to REYMENT & BENGTSON (1985), marine sedimentation on the Calabar Flank began with the deposition of the Odukpani Group (sensu PETTERS et al., 1995) in the mid-Albian linked to the separation of Africa from South America and the development of the South Atlantic Ocean. The Odukpani Group consists of the Albian platform carbonates of the Mfamosing Limestone and the Cenomanian Eze-Aku (Ekenkpon) Shales. Most of the fauna described in this paper was collected from and on the hardground, which separates the Mfamosing Limestone with sharp boundary from the overlying Eze-Aku Shales.

Locality details

As in other south-western African sedimentary basins, and in the Gulf of Guinea, marine sedimentation began in the Albian, associated with the opening of the South Atlantic Ocean and the separation of Africa from South America. The "Calabar Flank-carbonate platform" was established as a result of landward onlap of shallow marine carbonates onto the southern rim of the Oban Hills. Here, the Mfamosing Limestone was deposited on top of the fluvio-deltaic clastic sediments of the Awi Formation of probable Aptian age (ADELEYE & FAYOSE, 1978). The Mfamosing Limestone carbonate platform survived until the Upper Albian, when its existence was abruptly terminated, with the development of a hardground and omission surface from which most of the fauna dealt with in this paper was collected. Upper Albian ammonites are preserved as limestone moulds; Lower Cenomanian elements are phosphatised or pyritised and come from pockets in, and the surface of, the hardground.

In close cooperation with the Calcemco-geologists, Lobitzer carried out extensive field investigations and su-



pervised drilling programs for Calcemco in the wider surroundings of the Mfamosing Quarry in order to a better understanding of the spatial facies distribution of the succession. Even the deepest drill hole with approximately 140 m of section did not reach the crystalline basement complex of the Oban Hills. The Mfamosing Limestone, up to 80 m thick, rests on more than 15 m of probably Aptian-Albian cavernous dolomite, chalkified at some levels. From its classic locality the Mfamosing Limestone outcrop extends to the north-west, through Etankpini village (Text-Fig. 1) and beyond, along the southern slope of the Oban Hills. Our studies and those by AGBEBIA & EGESI (2017) and REIJERS & PETTERS (1997) confirm that karstification increases along strike. Furthermore, terrigenous-clastic input from the exposed hinterland of the Oban Hills becomes increasingly important along strike and landwards to the north. However, during transgressive phases, only minor amounts of siliciclastics accumulated in the Mfamosing Limestone.

The Mfamosing Limestone

The classical locality of the shallow-marine to intertidal Mfamosing Formation sensu PETTERS (1982) with the hardground at the top is the now abandoned Mfamosing quarry of Calabar Cement Company (Calcemco), (TextFig. 2). Here the limestones dip $5-10^{\circ}$ to the south-west. Meanwhile, the United Cement Company of Nigeria Ltd. (UniCem) has replaced the historic quarry with a new one.

The Mfamosing Limestone - the "Lower Limestone" sensu MURAT (1972a, b) - represents the northernmost carbonate deposit of the South Atlantic Ocean in West Africa. The Middle–Upper Albian stable carbonate platform of the Mfamosing Limestone was established during the initial marine transgression due to landwards onlapping of calcareous sediments on the "Calabar Flank" - the southern slopes of the Precambrian crystalline basement complex of the Oban Hills Massif. Structurally, the Calabar Flank is part of the foundered southeastern Nigerian Continental margin. The formation name "Mfamosing Limestone" has already been used in internal reports of Calcemco since 1976 and finally defined by PETTERS (1982). The Mfamosing Limestone represents the largest and chemically purest carbonate body in Nigeria, however, Calcemco was using this highest quality limestone for cement production alone. Time-equivalent carbonates occur on either side of the opening South Atlantic Ocean and are also well documented in several DSDP-, repectively ODP-Legs from the South Atlantic (e.g. PLETSCH et al., 1996, 2001).

At its classical section – the Mfamosing quarry – the Mfamosing Limestone records a wide variety of shallow ma-



Text-Fig. 2.

The Mfamosing Quarry in February 1976. The photo shows the general dip of the Mfamosing Limestone beds of approximately 9° in a south-westerly direction. A prominent hardground is developed at the top of the Mfamosing Limestone at this classic locality; this is the source of almost all of the Upper Albian and Lower Cenomanian fossils dealt with in this paper. The hardground is overlain by about 5 m of dark-grey to black shales of the Eze-Aku Formation, in turn overlain by about 10 m of coastal plain sands of the Benin Formation.

rine to intertidal depositional environments (REIJERS & PETTERS, 1987). In its upper part a significant influx of siliciclastics from the hinterland of the Oban Hills temporarily suppressed carbonate production. The Mfamosing Limestone is topped by an intraformational hardground (Text-Figs. 3, 4; FÖRSTER, 1978; FÖRSTER & SCHOLZ, 1979; OTI & KOCH, 1990).

REIJERS & PETTERS (1997), HARRY et al. (2017) deal with the sequence stratigraphic interpretation of the Mfamosing Limestone and the reason for the hardground on top of it, which they consider as product of a TST (transgressive systems tract), respectively of a MFS (maximum flooding surface). As REIJERS (1998) and PETTERS et al. (1995) pointed out, the influx of siliciclastics and sea-level fluctuations controlled carbonate production. Peritidal, lagoonal and reefal carbonates rim the igneous Oban Massif in the south and southwest and reflect an initial relative sea-level highstand. Maximal carbonate production took place during rising sea-level, when an open-marine carbonate platform and a mixed carbonate-siliciclastic shoal co-existed side by side.

According to ESSIEN & UFOT (2010) the age of the Mfamosing Limestone has been a subject of discussion by several researchers, who ascribed different ages based on different criteria. In his early papers, REYMENT (e.g. 1965) assigned a Cenomanian age to the Odukpani Formation, of which the Mfamosing Limestone is the basal unit. Following Reyment, DESSAUVAGIE (1968) erroneously regarded the foraminifer *Trocholina odukpaniensis* as Cenomanian. In the Mfamosing Limestone this characteristic foraminifer predominantly occurs in reef-like environments dominated by encrusting and ramose coralline red algae (FAYOSE, undated, ?1976; POIGNANT & LOBITZER, 1982). The latter formed



Text-Fig. 3. Mfamosing Quarry. Bedding plane surface of the hardground at the top of the Mfamosing Limestone with oyster shells and gastropods.

oncoidal algal packstones with dasycladaceans, stromatolitic and coralline algal boundstones, which point to a tidal flat environment; coralgal boundstones are rather rare. Also *Lithophaga*-borings occur relatively frequent in the coralline algal boundstones in the upper part of the Mfamosing Limestone and also in the hardground.

AKPAN (1992) recorded, for the first time, the itierid gastropod *Peruviella dolium* (RÖMER) from the basal section of the Mfamosing Limestone, and dated it as Mid-Albian on this basis. According to HANGER (1998), communities dominated by *P. dolium* are characteristic for Albian nearshore environments on both sides of the Cretaceous Tethyan seaway.

OTI & KOCH (1990) focused on the microfacies and diagenesis of the Mfamosing Limestone, which according to them was deposited during one Albian transgressive cycle. They concluded that the carbonates were deposited in a shallow shelf, characterized by strong lateral facies variations, with high-energy submarine bar carbonate sands, patch reefs, and algal boundstones.

The hardground at the top of the Mfamosing Limestone Formation

A remarkable colour contrast is evident between the top of the bright mud to wackestone of the Mfamosing Limestone and the approximately 30 cm thick, more intensively silicified rusty brown, ferruginous and in the upper part nodular phosphatic and pyritic mineralized hardground (Text-Figs. 3, 4). The stratigraphically condensed fossils on the bedding plane of the hardground – in particular ammonites, gastropods, scarce bivalves and echinoids, *Lithophaga* borings and *Thalassinoides*-burrows (AKPAN, 1990) – often show extensive corrosion due to omission and subsolution during the Albian-Cenomanian boundary interval. In contrast to the molluscs, the oyster shells are practically uncorroded, because they were probably growing on the already lithified hardground prior to the onset of sedimentation of the Eze-Aku Shales (Text-Figs. 2, 4). The hardground marks a transgressive event: a distinct sealevel rise during the Upper Albian-Lower Cenomanian interval. With the gradual drowning of the Mfamosing Limestone carbonate platform, an increase of terrigenous influx is evident and carbonate production ceased.

According to PALMER & WILSON (2004), carbonate hardgrounds often formed during calcite sea intervals, which were coincident with times of rapid seafloor spreading and global greenhouse climate conditions (STANLEY & HARDIE, 1999).

The Eze-Aku Shales

In the Mfamosing Quarry the hardground on top of the Mfamosing limestone is overlain unconformably with a sharp boundary by about five meters of black shales (Text-Fig. 2) of the Eze-Aku Formation sensu REYMENT (1965), repectively the Ekenkpon Formation sensu PETTERS et al. (1995). The Eze-Aku Formation is a sequence of pyritic and organic rich black shales, which locally shows minor intercalations of calcareous mudstones with oyster and inoceramid fragments and variable amounts of organic particles. The Eze-Aku Shales are the result of a second transgression on the Calabar Flank in the late Cenomanian.

Palynological studies by LAWAL (1991) demonstrate a Late Cenomanian age (*Triorites africaensis* Zone) for the basal Eze-Aku Formation in the lower Benue Trough. Based on ammonites and planktic foraminifera NYONG & RAMANATHAN (1985) consider the black organic-carbon-rich Eze-Aku Shales as sediments of a shallow epicontinental sea. It seems very likely that upwelling was responsible for these organic-rich sediments. All our samples of the Eze-Aku Shales analysed by HERBERT STRADNER (Geological Survey of Austria, Vienna) were barren of calcareous nannofossils.



Text-Fig. 4.

Mfamosing Quarry. The hardground at the top of the Mfamosing Limestone shows pyrite mineralization along vertical fractures and on the bedding plane. hardground is overlain with sharp boundary by organic-rich black shales of the Eze-Aku Formation. A late Cenomanian age is confirmed by the presence of the arenaceous foraminifer Thomasinella punica.

Above the Eze-Aku Formation about 10 m of red lateritic clays and coastal plain sands of the Benin Formation are exposed (Text-Fig. 2).

The Campanian–Maastrichtian Nkporo Shales cap the Cretaceous sequence of the Calabar Flank. They are, however, not exposed in the immediate environs of the Mfamosing quarry.

The first record of the foraminifer *Thomasinella punica* SCHLUMBERGER (original description by SCHLUMBERGER in THOMAS, 1893) in Nigeria – an indicator for a trans-Saharan seaway in the Late Cenomanian

REYMENT (1980) initiated the discussion of the timing of the first trans-Saharan transgression in connection with the opening of the South Atlantic Ocean. Ammonite and foraminifer data from the Gulf of Guinea and from adjacent African basins and also of ODP Leg 159 (e.g. MOULLADE et al., 1998) suggested that mid-or deep-water circulation between the equatorial and South Atlantic existed at least since the late Albian. At this time, faunal exchange along a trans-Saharan Seaway was minimal, if at all (e.g. BENGT-SON & KOUTSOUKOS, 1992; COURVILLE et al., 1998; PLETSCH et al., 1996, 2001). According to ZABORSKI (2000), an arm of the proto-Atlantic Ocean occupied the lower and middle Benue Trough in the upper Middle Albian, but the Upper Cenomanian transgression was more extensive and reached its acme in the Lower Turonian. During this epicontinental transgression, the sea entered from the Gulf of Guinea via the Calabar Flank into the Benue Trough and flooded the lullemmeden Basin (e.g. CHARRIÈRE et al., 1998: KOGBE, 1981: MEISTER & ABDALLAH, 1996: MEISTER et al., 1994,) and subsiding areas of the Sahara East of the Hoggar. Finally, it formed a short-lived connection between the Gulf of Guinea and the Tethys, and a faunal exchange was possible between the South Atlantic and the Tethys Ocean.

In this context an internal report from 1976 of the Geological Survey of Austria by Werner Fuchs (†) is relevent. He described a rich foraminiferan assemblage with hedbergellids, lenticulinids and the Cenomanian arenaceous taxon *Thomasinella punica* from the basal part of the anoxic black shales of the Eze-Aku Formation. It is probably the first record of this characteristic foraminifer from Nigeria. The assemblage indicates a shelf to upper slope depositional setting. ARNAUD-VANNEAU & PRESTAT (1984) report the occurrence of *Thomasinella punica* in other Southwest African coastal basins and in the context of the Congo Basin, MBANI (2008) stated "le Cénomanien est surtout caractérisé par *Thomasinella punica*". More recently, IGWE et al. (2015) and HARRY et al. (2017) dealt with the foraminifera fauna of the Eze-Aku Formation of the Lower Benue Trough.

Thomasinella punica is present in almost all our washed samples from the Eze-Aku Shales from the surroundings of the Mfamosing quarry, however, only in the coarse grain fraction. Therefore the statement by MBANI (2008) is true also for the Calabar Flank.

Age and affinities of the faunas

The faunas described below can be dated in terms of the zonal scheme set out in Table 1, based on the sequence established in Western Europe (KENNEDY & GALE, 2015, 2017).

The oldest fauna recognized from the hardground is preserved as limestone moulds comprises *Pervinquieria* (*Subschloenbachia*) *rostrata* (J. SOWERBY, 1817) (Text-Figs. 8, 9), and, possibly, *Arestoceras* sp. (Text-Fig. 12). The former indicates the presence of the Upper Albian *rostrata* Zone of the standard sequence, and has a cosmopolitan distribution including Western Europe eastwards to Iran, Japan, Tamil Nadu in South India, Madagascar, and Texas. *Arestoceras* is best known from KwaZulu-Natal in South Africa; records from elsewhere are doubtful.

The presence of the succeeding Upper Albian *perinflata* Zone is indicated by the presence of a single individual (Text-Fig. 10) preserved as limestone internal mould, compared to the index species, which is again cosmopolitan, with records of the species, or close allies, from Western Europe to Ukraine (Crimea), Texas, and KwaZulu-Natal in South Africa and, possibly Iran and Tamil Nadu in south India.

The Lower Cenomanian fauna is:

Puzosia (Anapuzosia) sp.

Stoliczkaia (Lamnayella) juigneti (WRIGHT & KENNEDY, 1978) Salaziceras nigerianum FÖRSTER & SCHOLZ, 1979

SUBSTAGE	ZONE	SUBZONE
	Mantelliceras dixoni	
	Mantelliceras mantelli	Mantelliceras saxbii
Lower Cenomanian		Sharpeiceras schlueteri
		Neostlingoceras carcitanense
Upper Albian (part)	Pleurohoplites briacensis	
	Pervinquieria (S.) perinflata	
	Pervinquieria (S.) rostrata	
	Pervinquieria (S.) fallax	
	Pervinquieria (S.) inflata	

Tab. 1.

Upper Albian and Lower Cenomanian ammonite zonation used in the present study.



The material occurs in three preservations, phosphatic internal moulds, pyritic nuclei, and crushed, unphosphatised material. The last two preservation categories are interpreted as the youngest elements of the fauna. They include Graysonites wacoense (unphosphatised) and Stoliczkaia (Lamnayella) juigneti (a pyritic nucleus), the latter a species restricted to the carcitanense Subzone of the Lower Cenomanian mantelli Zone, which sets an upper age limit for the assemblage. Of other species known from localities other than south-eastern Nigeria, all are restricted to the Lower Cenomanian, and most have wide geographic distributions. Of the remainder, Flickia bullata sp. nov. belongs to a genus that is known from the Upper Albian and Lower Cenomanian of Algeria, Tunisia, Texas, KwaZulu-Natal in South Africa, and Madagascar, whilst bullata is most closely related to Flickia quadrata COLLIGNON, 1964 (23, Pl. 322, Figs. 1428, 1429) known only from the Lower Cenomanian of Madagascar (WRIGHT & KENNEDY, 1979 revise the genus Flickia and its constituent species). Its presence is compatible with the Lower Cenomanian assignation of the fauna. Acompsoceras calabarense belongs to a genus known from the Lower Cenomanian of Western Europe, Tunisia, Texas, and Madagascar. Sharpeiceras nigeriense belongs to an even more widely distributed genus, with records from Western Europe eastwards to Kazakhstan and Iran, Texas and northern Mexico, the Middle East, North Africa, KwaZulu-Natal in South Africa, Madagascar, Tamil Nadu in South India, and Japan.

There remains *Salaziceras nigerianum* FÖRSTER & SCHOLZ (1979: 111) argued for this as an Upper Albian element in the fauna, although the preservation of the types is that of other, unequivocally Lower Cenomanian taxa, rather than the unequivocally Upper Albian taxa present. Furthermore, since the original account of *Salaziceras nigerianum* in 1979, the genus has been recognized in the Upper Albian of Madagascar (KENNEDY & KLINGER, 2008) and Lower Cenomanian of northern KwaZulu-Natal in South Africa (KENNEDY & KLINGER, 2012).

In conclusion, the ammonites faunas from the Mfamosing Quarry belong, predominantly, to cosmopolitan genera and species, suggesting free communication from both north and south during the Upper Albian and Lower Cenomanian.

FÖRSTER & SCHOLZ (1979: 111) argued for the presence of representative elements of the *briacensis* Zone of SCHOLZ (1973) in the Mfamosing faunas, placing special weight on the presence of *Salaziceras*. This is problematic, in that they do not record any of the species upon which Scholz based

his *briacensis* Zone, while this zone spans the Albian/Cenomanian boundary in the Global boundary Stratotype Section for the base of the Cenomanian Stage (KENNEDY et al., 2004). The index species is currently referred to the genus *Pleurohoplites* SPATH, 1921 (see KENNEDY, 2015: 409 et seq.), which is restricted to the Old World Boreal Realm. Equally absent from the Mfamosing faunas are elements from the North African equivalent of the *briacensis* Zone, the *Stoliczkaia* (*Shumarinaia*) *africana* Partial Range Zone of ROBASZYNSKI et al. (2008). There is thus no evidence for the presence of unequivocal *briacensis* Zone elements in the faunas from the Mfamosing Quarry.

Conventions

Dimensions are given in millimeters: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in parentheses are dimensions as a percentage of the diameter. The suture terminology is that of KORN et al. (2003): E = external lobe; A = adventive lobe (= lateral lobe, L, of KULLMANN & WIEDMANN 1970); U = umbilical lobe; I = internal lobe.

Repositories of specimens

- BMNH: The Natural History Museum, London.
- BSPHG: Bayerische Staatsammlung für Paläontologie und historische Geologie, Munich.
- EMP: Collections of the École des Mines, Paris, currently housed in the collections of the Université Claude Bérnard, Lyon.
- FSM: Collections of the Faculté des Sciences, Le Mans.
- GBA: Geologische Bundesanstalt, Vienna.
- MGL: Musée Geologique, Lausanne.
- MNHG: Muséum d'Histoire Naturelle, Genève.
- MNHN: Laboratoire de Paléontologie of the Muséum nationale d'Histoire Naturelle, Paris.
- OUMNH: Oxford University Museum of Natural History.
- TMM: Texas Memorial Museum, Austin, Texas.
- USNM: US National Museum of Natural History, Washington D.C.

Systematic palaeontology

Order Nautilida DE BLAINVILLE, 1825 Suborder Nautilina DE BLAINVILLE, 1825 Superfamily Nautiloidea DE BLAINVILLE, 1825 Family Cymatoceratidae SPATH, 1927 Genus *Cymatoceras* HYATT, 1884

Type species: *Nautilus pseudoelegans* D'ORBIGNY, 1840: 70, Pl. 8, Figs. 1–4; Pl. 9, Figs. 1, 2, by the original designation of HYATT (1884: 301).

Cymatoceras sakalavum (COLLIGNON, 1949)

(Text-Figs. 5A-D)

1949 *Nautilus (Cymatoceras) sakalavum* COLLIGNON: 41, PI. 6, Figs. 1, 2; PI. 21, Fig. 1.

1979 Cymatoceras sp. FÖRSTER & SCHOLZ: 117.

Type: The holotype, by original designation, is the original of COLLIGNON (1949: 41, Pl. 6, Fig. 2) from the Lower Albian of Ambaramaninga, Madagascar, in the collections of the École Nationale Supérieur des Mines, now housed in the collections of the Université de Lyon I, Villeurbanne (EMP).

Material: GBA 2016/003/0001-0003.

Description: GBA 2016/003/0001 (Text-Figs. 5A–B) is an internal mould of a 180° sector of phragmocone with an estimated original diameter of 70 mm approximately. Coiling is very involute, the umbilicus very small and deep. The whorl section is depressed, with a whorl breadth to height ratio of 1.1, the greatest breadth just outside the umbilical shoulder, the flanks feebly convex and converging to the broadly rounded ventrolateral shoulders and venter. The low ribs broaden rapidly across the flanks, and are markedly convex across the ventrolateral shoulders, crossing the venter in a marked concavity.

GBA 2016/003/0003 (Text-Figs. 5C–D) is an internal mould of an incomplete half whorl of body chamber with an estimated original diameter of 120 mm. The original whorl section was depressed, although the original proportions cannot be established. The flanks are convergent and very feebly convex, the venter very broad and feebly convex. The course of the low ribs is clearer than in the previous specimen, straight and rursirdiate on the inner flank, flexing back and broadening markedly on the middle and outer flanks and venter, sweeping back and convex on the outer flank, and markedly concave on the venter, where they are at their broadest.

The siphuncle is in a slightly dorsal position in GBA 2016/003/0002. The suture (Text-Figs. 5A, B) is very feebly concave across the flanks, very feebly convex across the ventrolateral shoulder, and near-straight over the venter.

Discussion: These specimens are referred to *Cymatoceras* sakalavum on the basis of relative proportions, form and course of the low, wide ribs. There are similarities to *Cymatoceras imbricatus* (CRICK, 1907: 220, Pl. 14, Fig. 6), from the presumed Cenomanian of northern KwaZulu-Natal in

South Africa in both the width and course of the ribs, but the whorl section is compressed rather than depressed, as in the present species. *Cymatoceras striatocostatus* (CRICK, 1907: 221, Pl. 14, Fig. 7) from the same locality and horizon as *C. imbricatus*, has a depressed whorl section, but the ribs are even broader than those of the present species.

Occurrence: Middle Albian of Madagascar, Lower Cenomanian of Nigeria.

Order Ammonoidea ZITTEL, 1884 Suborder Ammonitina HYATT, 1889 Superfamily Desmoceratoidea ZITTEL, 1895 Family Puzosiinae SPATH, 1922 Subfamily Puzosiinae SPATH, 1922 Genus *Puzosia* BAYLE, 1878

Type species: *Ammonites planulatus* J. DE C. SOWERBY, 1827: 134, PI. 570, Fig. 5, non SCHLOTHEIM, 1820: 59; = *Ammonites mayorianus* D'ORBIGNY, 1841: 267, PI. 79, Figs. 1–3, by subsequent designation by H. DOUVILLÉ (1879: 91).

Subgenus Anapuzosia MATSUMOTO, 1954

Type species: *Puzosia buenaventura* ANDERSON, 1938: 185, Pl. 40, Fig. 3; Pl. 41, Figs. 1, 2, by the original designation of MATSUMOTO (1954: 71).

Puzosia (Anapuzosia) sp.

(Pl. 1, Figs. 6–14; Text-Figs. 6, 7)

Material: GBA 2016/003/0011-0021.

Description: The earliest growth stages seen are represented by GBA 2016/003/0012-0017, which range from 30 to 53 mm in diameter. Coiling is moderately involute, the umbilicus comprising 30 % approximately of the diameter, shallow, with a low, flattened wall and narrowly rounded umbilical shoulder. The whorl section is slightly compressed, with whorl breadth to height ratios of up to 0.9, the inner to mid-flank region feebly convex, the outer flanks converging to broadly rounded ventrolateral shoulders and a feebly convex venter. Ornament is best preserved in GBA 2016/003/0016 (Pl. 1, Figs. 6, 7). Strong collar ribs precede feeble constrictions. The ribs are prorsiradiate, feebly convex on the inner flank, flexed back and concave on the outer flank, and flexed forwards over the ventrolateral shoulder. The collar ribs are separated by much finer ribs that are very weak to obsolete on the inner flank, strengthening at mid-flank and increasing by branching and intercalation. A distinctive feature is that some ribs bifurcate on the ventrolateral shoulder (PI. 1, Fig. 12). Poor preservations precludes determination of the number of fine ribs between successive constrictions and collar ribs, but there are both coarser (PI. 1, Figs. 6, 7) and finer and more densely ribbed individuals (Pl. 1, Figs. 8).





There are two much larger specimens. GBA 2016/003/0018 (Pl. 1, Fig. 13) is a crushed individual, 135 mm in diameter. Parts of two collar-ribs, 45° approximately apart, are preserved on the adapical part of the specimen, with an estimated 14 or more weaker ribs between at the ventrolateral shoulder. The ribs are markedly flexuous, and increase by branching and intercalation, in some cases on the ven-

trolateral shoulder. GBA 2016/003/0019 (Text-Fig. 6) is an undeformed individual retaining extensive areas of replaced shell, the ventrolateral and ventral ornament well preserved. The ribbing is finer than in the previous specimen, with 13 weaker ribs between successive constrictions and collar ribs.



Puzosia (Anapuzosia) sp. GBA 2016/003/0019. Figures are x 1.

A juvenile suture is shown in Text-Figure 7; E/A and A/U2 are deeply incised, narrow-stemmed, and bifid; A and U2 are deeply incised, and trifid.

Discussion: The present material is interpreted as a variable species with both finer and coarser ribbed individuals. It is referred to *Anapuzosia* in the basis of the whorl section, crowded sinuous ribs and strong collar ribs. Of

described species, it most closely resembles *Puzosia* (*Anapuzosia*) *multicostata* RENZ, 1972 (707, Pl. 2, Figs. 1, 2; Pl. 3, Fig. 1; Pl. 9, Fig. 4; Text-Figs. 2b, 3) from the Upper Albian of Venezuela, but this has up to 24 ribs between successive collar ribs and constrictions. The present rather poor material is left in open nomenclature.

Occurrence: As for material.



Text-Fig. 7. Partial external suture of *Puzosia* (*Anapuzosia*) sp. GBA 2016/003/0012.

Superfamily Acanthoceratoidea DE GROSSOUVRE, 1894

Family Brancoceratidae SPATH, 1934 Subfamily Mortoniceratinae H. DOUVILLÉ, 1912 Genus *Pervinquieria* ВÖHM, 1910

Type species: *Ammonites inflatus* J. SOWERBY, 1817: 170, Pl. 178, by the original designation of BÖHM (1910: 152).

Subgenus Subschloenbachia SPATH, 1921 (= Durnovarites SPATH, 1932: 380)

Type species: *Ammonites rostratus* J. SOWERBY, 1817: 163, Pl. 173, by the original designation of SPATH (1921: 284).

Pervinquieria (Subschloenbachia) rostrata (J. SOWERBY, 1817)

(Text-Figs. 8, 9)

- 1817 Ammonites rostratus J. SOWERBY: 163, Pl. 173.
- 2018 Mortoniceras (Mortoniceras) rostratum (J. SOWERBY, 1817); KLEIN: 101, 122 (with full synonymy).
- 2019 Pervinquieria (Subschloenbachia) rostrata (J. SOWERBY, 1817); GALE et al.: 214, Pl. 13; Pl. 14, Figs. 1, 2.

Type: The holotype, by monotypy, is OUMNH K.835, the original of *Ammonites rostratus* J. SOWERBY, 1817: 163, Pl. 173, from the Upper Greensand of Roke, 1.5 km NNE of Benson, Oxfordshire, refigured by KENNEDY et al. (1998: Figs. 9–11).

Material: GBA 2016/003/0004, 0005, 0007.



Text-Fig. 8. Pervinquieria (Subschloenbachia) cf. rostrata (J. SOWERBY, 1817), GBA 2016/003/0005. Figures reduced x 0.5; the original is 300 mm in diameter.



Text-Fig. 9. Pervinquieria (Subschloenbachia) rostrata (J. SowER-BY, 1817), GBA 2016/003/ 0004. Figures are reduced x 0.7; the original is 215 mm in diameter.

Description: The specimens are very poorly preserved, the largest 300 mm in diameter (Text-Fig. 8). The bestpreserved fragment is GBA 2016/003/0004 (Text-Fig. 9), a 180° whorl sector with a maximum preserved diameter of 220 mm. Coiling is very evolute, the shallow umbilicus comprising 41 % of the diameter. The original whorl section has been modified by abrasion. The flanks are flattened, the ventrolateral shoulders broadly rounded; there is a strong siphonal keel. There are nine primary ribs on the fragment. Most arise on the umbilical wall and strengthen into a coarse umbilical bulla; others lack a bulla. Most of the bullae give rise to a single rib, with a pair arising from a bulla at the adapical end. The ribs are coarse, broad, straight, prorsirdiate, and bear a coarse outer lateral bulla, coarse rounded inner ventrolateral tubercle and a coarse outer ventrolateral clavus.

Discussion: The coarse ribbing and tuberculation of these poor specimens corresponds to that of the body chamber of the holotype (KENNEDY et al., 1998: Text-Figs. 9–11) and comparable specimens from Texas (KENNEDY et al., 1998: Text-Fig. 13; KENNEDY in KENNEDY et al., 2005: Text-Fig. 12).

Occurrence: Index of the eponymous uppermost Albian zone, the geographic distribution extends from southern England to France, Spain, Germany, Switzerland, Hungary, Serbia, Ukraine (Crimea), Romania, Bulgaria, Turkmenistan, northern Iran, southern Tibet, Texas, Angola, Nigeria, Tamil Nadu in south India, Texas in the United States, and Japan.

Pervinquieria (Subschloenbachia) cf. perinflata (SPATH, 1921)

(Text-Fig. 10)

Compare:

- 1860 Ammonites inflatus PICTET & CAMPICHE (non J. SOWER-BY): PI. 21, Fig. 5; PI. 22, Fig. 3.
- 1921 Subschloenbachia perinflata SPATH: 284.
- 2018 Mortoniceras (Durnovarites) adkinsi (YOUNG, 1957); KLEIN: 137, 138 (with synonymy).
- 2018 *Mortoniceras (Durnovarites) depressum* SPATH, 1922; KLEIN: 137, 139 (with synonymy).

- 2018 Mortoniceras (Durnovarites) perinflatum (SPATH, 1921); KLEIN: 137, 140 (with full synonymy).
- 2018 *Mortoniceras (Durnovarites) quadratum* SPATH, 1922; KLEIN: 138, 142 (with synonymy).
- 2018 Mortoniceras (Durnovarites) subquadratum crassicostatum SPATH, 1933; KLEIN: 138, 143 (with synonymy).
- 2018 Mortoniceras (Durnovarites) subquadratum subquadratum SPATH, 1933; KLEIN: 138, 145 (with synonymy).
- 2018 *Mortoniceras (Durnovarites) subquadratum tumidum* SPATH, 1933; KLEIN: 138, 143 (with synonymy).
- 2018 *Mortoniceras (Durnovarites) vraconense* RENZ, 1968; KLEIN: 138, 145 (with synonymy).

Type: The holotype, by monotypy, is the original of PICTET & CAMPICHE 1860 (Pl. 22, Fig. 3), in the collections of the Muséum d'Histoire Naturelle, Geneva, from the Upper Albian of La Vraconne, Saint Croix, Switzerland. It was refigured by RENZ (1968: Pl. 9, Fig. 1), WIEDMANN & DIENI (1968: Pl. 14, Fig. 4) and MEISTER et al. (2011: Text-Figs. 5a, b).

Material: BMNH C83089, collected by P.M.P. Zaborski from the top surface of the main limestone in the Mfamosing Formation of the Mfamosing Quarry.

Description: BMNH C83089 (Text-Fig. 10) is a 180° whorl sector with a maximum preserved diameter of 160 mm, worn on one flank, the umbilicus concealed by matrix. The flattened outer flanks converge to broadly rounded ventrolateral shoulders. The venter is feebly convex in intercostal section, with a coarse siphonal keel. Strong, coarse umbilical bullae give rise to very strong straight prorsiradiate ribs that alternate regularly with single coarse intercalated ribs to give a total of 12 at the ventrolateral shoulder of the fragment. The adapical primary rib has a small lateral tubercle; on the succeeding primary ribs, the tubercle is developed as a low, broad bulla. All ribs bear a strong conical inner ventrolateral tubercle, linked by a broad prorsiradiate rib to a coarse outer ventrolateral clavus, from which a broad rib sweeps forwards and effaces before reaching the siphonal keel.



Text-Fig. 10.

Pervinquieria (Subschloenbachia) cf. perinflata (SPATH, 1921), BMNH C83089, collected by P.M.P. Zaborski from "the top surface of the main limestone of the Upper Albian Mfamosing Formation at the Mfamosing Quarry". Figures are x 1 (photos courtesy of the Natural History Museum, London). **Discussion:** The presence of four rows of tubercles in BMNH C83089 indicated in to be a *Mortoniceras* (*Subschloenbachia*). The relatively stout whorl section and coarse tuber-culation correspond to that of the holotype of *P.* (*S.*) *perinflata* (see above), which is a phragmocone.

Occurrence: Upper Upper Albian, index of the eponymous zone, with records from southern England, southeastern France, Switzerland, Ukraine (Crimea), Hungary, Texas in the United States, Nigeria, KwaZulu-Natal in South Africa, and, possibly, Iran and Tamil Nadu, south India.

Pervinguieria (Subschloenbachia) sp.

(Text-Fig. 11)

Material: GBA 2016/003/0009, collected ex situ.

Description: The specimen (Text-Fig. 11) is a 180° sector of body chamber 150 mm in diameter, with one flank and the venter very well preserved. The whorl section is rounded-trapezoidal, with feebly convex convergent flanks and broadly rounded ventrolateral shoulders; there is a strong siphonal keel. Coiling is moderately evolute, the umbilicus quite deep, comprising 31 % of the diameter, with a convex wall and quite narrowly rounded umbilical shoulder. Six well-developed umbilical bullae are preserved on the penultimate half whorl. There are six umbilical bullae of variable strength on the outer half whorl that give rise pairs of ribs, with, in one case, a third rib tenuously attached; there are also long and short ribs, to give a total of 16 ribs at the ventrolateral shoulder. There are faint suggestions of a lateral and inner ventrolateral tubercle, and all ribs bear a well-developed outer ventrolateral clavus.

Discussion: Umbilical and outer ventrolateral tubercles are well defined, but there are only very feeble indications of a lateral and inner ventrolateral row, perhaps a reflection of the specimen being a possibly adult body chamber. Accordingly, it is referred to *Subschloenbachia* with caution.

Occurrence: As for material.



Genus Arestoceras VAN HOEPEN, 1942

Type species: *Arestoceras collinum* VAN HOEPEN, 1942: 118, Text-Figs. 104–109, by original designation.

Arestoceras sp.

(Text-Fig. 12)

Material: GBA 2016/003/0008.

Description: The specimen is a poorly preserved, badly worn internal mould of a 180° sector of phragmocone with a maximum preserved diameter of 126 mm. The whorl section is estimated to have been as wide as high, the inner to mid-flanks feebly convex, the outer flanks converging to broadly rounded ventrolateral shoulders, the venter very feebly convex in intercostal section and broadly fastigiate in costal section, with a coarse siphonal keel. There are estimated 14–17 ribs at the ventral shoulder. The umbilical region is not preserved. The ribs are straight and prorsiradiate on the inner flank, broaden and sweep forwards

on the outer flank, and link to blunt, oblique ventrolateral clavi. The clavi give rise to a strongly prorsirsdiate rib that effaces before reaching the siphonal keel.

Discussion: The presence of a single row of ventrolateral tubercles and asbsence of lateral tubercles suggest *Arestoceras*, the specimen most closely resembling the *Arestoceras* sp. nov. of MEISTER et al. (2011: 693, PI. 6, Fig. 2), from the Upper Albian of the Sumbe region in Cuanza Sul Province, Angola.

Occurrence: As for material.



Text-Fig. 12. Arestoceras sp. GBA 2016/003/0008. Figures are x 1.

Family Lyelliceratidae SPATH, 1921 Subfamily Stoliczkaiinae BREISTROFFER, 1953 Genus *Stoliczkaia* NEUMAYR, 1875

Type species: *Ammonites dispar* D'ORBIGNY, 1841: 142, Pl. 45, Figs. 1, 2, by the original designation of NEUMAYR (1875: 179).

Subgenus Lamnayella WRIGHT & KENNEDY, 1978

Type species: *Stoliczkaia* (*Lamnayella*) *juigneti* WRIGHT & KEN-NEDY, 1978: 398, PI. 37, Figs. 1–10, PI. 38, Figs. 1–12, by the original designation of WRIGHT & KENNEDY (1978: 394).

Stoliczkaia (Lamnayella) juigneti WRIGHT & KENNEDY, 1978

(Text-Figs. 13A-D, I)

- 1978 Stoliczkaia (Lamnayella) juigneti WRIGHT & KENNEDY: 398, Pl. 37, Figs. 1–10; Pl. 38, Figs. 1–12; Text-Figs. 4a–c.
- 2018 Stoliczkaia (Lamnayella) juigneti WRIGHT & KENNEDY, 1978; KLEIN: 235, 237 (with full synonymy).

Types: The holotype, by original designation, is MNHN. F. A27381, the original of Wright & Kennedy (1978: 398, Pl. 37, Figs. 1–4); it and paratypes MNHN. F. A27382–4 and FSM 117 and 173 are from the Lower Cenomanian *Neostlingoceras carcitanense* Subzone of the *Mantelliceras mantelli* Zone, Craie Glauconieuse à *Pecten asper* Lamnay, Sarthe, France.

Paratype BMNH C83578 is from the *carcitanense* Subzone fauna of the basement bed of the Wilmington Sands at Hutchin's Pit, Wilmington, Devon.

Material: GBA 2016/003/0022-0026.

Description: The earliest growth stages are represented by GBA 2016/003/0022 (Text-Fig. 13D) and the nucleus of GBA 2016/003/0023 (Text-Figs. 13A, I). The former is a pyritised individual 12 mm in diameter, the umbilicus obscured by pyrite overgrowths. Coiling is very involute, the umbilicus tiny. The whorl section is very compressed, the flanks very feebly convex and subparallel, the ventrolateral shoulders quite narrowly rounded, the narrow venter feebly convex. Delicate falcoid riblets arise on the umbilical shoulder, strengthen across the flanks and develop into relatively broad concave outer flank ribs, 14 on the outer half whorl, that terminate in sharp ventral clavi. The venter is raised into a blunt siphonal ridge. The nucleus of GBA 2016/003/0023 (Text-Figs. 13A, I) has coarse concave ribs on the outer flank. The fragmentary outer whorl of this specimen has an estimated diameter of 43 mm, and retains a short sector of the body chamber. Coiling is only moderately involute, the umbilicus shallow, comprising 20 % of the diameter, the wall low, and outwardinclined in intercostal section. The whorl section is compressed, the intercostal section with feebly convex flanks, broadly rounded ventrolateral shoulders and a feebly convex venter. The costal whorl breadth to height ratio is 0.8 approximately, the greatest breadth at the umbilical bullae. Primary ribs arise at the umbilical seam, and strengthen into prominent bullae that give rise to relatively coarse primary ribs, while up to three long and short ribs intercalate between successive primaries, all ribs strengthening into a feeble ventral bulla that is little more than an an-



Text-Fig. 13.

A–D, I: Stoliczkaia (Lamnayella) juigneti WRIGHT & KENNEDY, 1978. A, B, I: GBA 2016/003/0023; C: GBA 2016/003/0024; D: GBA 2016/003/0022, E–H: Utaturiceras sp. E, F: GBA 2016/003/0038; G, H: GBA 2016/003/0039. Figures A–C, E–H are x 1; D and I are x 2.

gulation in the rib profile; the venter is feebly fastigiate in costal section. The largest fragment, GBA 2016/003/0024 (Text-Fig. 13C) has a maximum preserved whorl height of 20 mm and is part body chamber.

Discussion: The species is discussed at length by WRIGHT & KENNEDY (1978: 398; 1984: 77), to whom reference should be made.

Occurrence: Lower Cenomanian of southern England, Sarthe in France, and now Nigeria.

Family Flickiidae ADKINS, 1928 Subfamily Salaziceratinae, KENNEDY & WRIGHT, 1984

Genus Salaziceras BREISTROFFER, 1936

Type species: Ammonites salazacensis HÉBERT & MUNIER-CHALMAS, 1875: 114, Pl. 5, Fig. 6, by the original designation of BREISTROFFER (1936: 64).

Salaziceras nigerianum FÖRSTER & SCHOLZ, 1979

(Pl. 2, Figs. 14-22)

- 1979 Salaziceras nigerianum FÖRSTER & SCHOLZ: 113, Text-Figs. 1–3.
- 2018 Salaziceras (Salaziceras) nigerianum FÖRSTER & SCHOLZ, 1979; KLEIN: 246, 247 (with synonymy).

Type: The holotype, by original designation is BSPHG. 1978 X 1, the original of FÖRSTER & SCHOLZ (1979: Text-Figs. 2b, 3, 5) from the Mfamosing Quarry. The specimen was collected by Lobitzer and after the early death of R. Förster, was presented to the Bayerische Staatssammlung für Paläontologie und historische Geologie in Munich.

Material: GBA 2016/003/0027-0033.

Description: Coiling is evolute, the umbilicus comprising an estimated 40 % of the diameter in GBA 2016/003/0030 (Pl. 2, Fig. 19), and of moderate depth. The whorl section is depressed reniform, with costal whorl breadth to height ratios of up to 1.3. On phragmocone fragments, an estimated five coarse primary ribs per half whorl arise at the umbilical seam, sweep forwards across the umbilical wall, and strengthen into prominent umbilical bullae. These give rise to prorsiradiate ribs, either singly or in pairs, with occasional intercalated ribs. The ribs flex forwards on the ventrolateral shoulder, and cross the venter in a feeble convexity. GBA 2016/003/0030 (Pl. 2, Fig. 19), is interpreted as an adult body chamber. Ornament on the adapertural part is as on the phragmocone, but weakens rapidly thereafter to feeble umbilical bullae and flank ribs, the venter near-smooth at the greatest preserved diameter. The suture (FÖRSTER & SCHOLZ, 1979: Text-Fig. 2) is little incised, with bifid A and U_2 .

Discussion: The diagnostic feature of *Salaziceras nigerianum* is the prominent umbilical bullae that give rise to pairs of ribs. FÖRSTER & SCHOLZ (1979: 114) discuss differences between the present species and others referred to the genus.

Occurrence: As for material.

Subfamily Flickiinae ADKINS, 1928 Genus *Flickia* PERVINQUIÈRE, 1907

Type species: *Flickia simplex* PERVINQUIÈRE, 1907: 214, Pl. 9, Figs. 2–5; Text-Figs. 80, 82, by monotypy.

Flickia bullata sp. nov.

(Pl. 1, Figs. 1–5)

1986 Flickia quadrata ZABORSKI, non COLLIGNON: 374, Text-Figs. 1d, e; 2m-q.

Types: The holotype is GBA 2016/003/0010 (Pl. 1, Figs. 3–5); it and paratype GBA 2016/003/0011. Other paratypes are BMNH C90374 and C90375, from the Lower Cenomanian part of the Odukpani Formation in cuttings on the Calabar-Akampka road, 1.5 km north of the junction with the Calabar-Ikot Ekpene road, in Cross River State, Nigeria.

Diagnosis: A *Flickia* with umbilical bullae on the phragmocone.

Description: The holotype (Pl. 1, Figs. 3-5) is a pyritic internal mould of an adult with a maximum preserved diameter of 19.5 mm. Coiling is moderately involute, the umbilicus comprising 30 % approximately of the diameter, shallow, with a flattened wall and broadly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.8 approximately. The flanks are flattened and subparallel, the ventrolateral shoulders broadly rounded, the venter feebly fastigiate, and feebly convex on either side of the line of the mid-venter. There are six umbilical bullae on the adapertural 90° sector of the penultimate whorl and the adapical 120° sector of the outer whorl. The bullae give rise to low, broad, feeble prorsiradiate ribs that efface on the outer flanks. The bullae are lost on the body chamber, their place taken by low, broad, crowded prorsiradiate ribs that efface on the outermost flanks. There is a single broad, shallow constriction on the ventrolateral shoulders and venter 60° from the apertural end of the body chamber. Paratype GBA 2016/003/0011 (Pl. 1, Figs. 1, 2) is a pyritic internal mould of a 180° whorl sector 14.2 mm in diameter, and almost entirely adult body chamber. Ornament corresponds to that of the holotype. The suture (ZABORSKI, 1986: Text-Figs. 1d, e) has entire elements, as is typical for the genus, with a relatively large E/A and a smaller A/U_2 .

The considerable size difference between these two specimens described here may be an indication of dimorphism.

Discussion: The species is clearly closely related to *Flickia quadrata* COLLIGNON, 1964 (23, Pl. 322, Figs. 1428, 1429, refigured by WRIGHT & KENNEDY, 1987: 695, Pl. 88, Figs. 27–37), notably in the presence of a broad constriction on the ventrolateral shoulders and venter of the body chamber, but they differ in the absence of umbilical bullae in *quadrata*.

Occurrence: As for types.

Family Acanthoceratidae DE GROSSOUVRE, 1894 Subfamily Mantelliceratinae HYATT, 1903 Genus *Graysonites* YOUNG, 1958

Type species: *Graysonites lozoi* YOUNG, 1958: 172, Pl. 27, Figs. 1–11, Text-Figs. 1b, c, d, f, by original designation = *Mantelliceras wacoense* BÖSE, 1928: 215, Pl. 5, Figs. 9–25; Pl. 6, Figs. 1–4.

Graysonites wacoense (BÖSE, 1928)

(Pl. 4, Figs. 1, 2, 6–8)

- 1928 Mantelliceras wacoensis Böse: 215, Pl. 5, Figs. 9–25; Pl. 6, Figs. 1–4.
- 2005 Graysonites wacoense (BÖSE, 1928); KENNEDY in KENNE-DY et al.: 390, Text-Figs. 24a, b; 26–32; 33d–f; 34– 38 (with full synonymy).
- 2015 Graysonites wacoense (Böse, 1928); Kennedy: 404, Text-Figs. 157g–I.

Types: The holotype is TMM 21610, the original of BÖSE (1928: Pl. 5, Figs. 9, 10, 23, 24); paratypes are TMM 21611–4. All are from the lower Lower Cenomanian Del Rio Clay on the east side of the Santa Fe track, 7.4 km (4.5 miles) south of McGregor, McLennan County, Texas.

Material: GBA 2016/003/0034-0037.

Description and Discussion: GBA 2016/003/0034-0035 are very crushed fragments. The latter (PI. 4, Fig. 8), 68 mm in diameter, shows the coiling to have been involute, the umbilicus comprising 22 % approximately of the diameter. Eight primary ribs arise at the umbilical seam, strengthen across the umbilical wall, and develop into elongate umbilical bullae. These give rise to narrow, straight primary ribs, either singly or in pairs, with additional ribs intercalating. The ribs strengthen across the flanks, and link to well-differentiated inner ventrolateral bullae. The ventral region is not preserved on this specimen, which compares well with USNM 520209 (KENNEDY in KENNEDY et al., 2005: Text-Figs. 29g-i; KENNEDY, 2015: Text-Figs. 157i-l). GBA 2016/003/0036 (Pl. 4, Figs. 6, 7) is a phragmocone fragment with a maximum preserved diameter of 115 mm and comparable if worn ornament. The ventrolateral and ventral regions are well preserved, with weak inner ventrolateral bullae linked by a strong prorsiradiate rib to stronger outer ventrolateral clavi. GBA 2016/003/0037 (Pl. 4, Figs. 1, 2) is a phragmocone fragment 101 mm long, lacking the inner flank region. The ornament is comparable in style to that of the previous specimens, but much more subdued, the weak inner ventrolateral bullae progressively effacing to a mere angulation in the rib profile. This specimen corresponds closely to USNM 520210, the original of KENNEDY in KENNEDY et al. (2005: Text-Fig. 36).

Occurrence: Lower Lower Cenomanian of Texas, California, southern England, and Nigeria.

Genus Utaturiceras WRIGHT, 1956

Type species: *Ammonites vicinalis* STOLICZKA, 1864: 84, Pl. 44, Figs. 1, 4, 5, 7, 8, non 2, 3, 6, by the original designation of WRIGHT (1956: 392).

Utaturiceras sp.

(Text-Figs. 13E-H)

Material: GBA 2016/003/0038-0039.

Description and Discussion: GBA 2016/003/0038 (Text-Figs. 13E, F) is a 120° whorl sector of phragmocone with a maximum preserved whorl height of 34 mm approximately. Coiling is very involute with a tiny, shallow umbilicus. The whorl section is compressed, with a whorl breadth to height ratio of 0.7 approximately. The umbilical shoulder is guite narrowly rounded, the inner and middle flanks flattened and subparallel, the outer flanks converging to broadly rounded ventrolateral shoulders, the venter flattened, with a feeble siphonal ridge. There are three weak umbilical bullae on the fragment. They give rise to pairs of very feeble ribs, with additional ribs intercalating, to give a total of an estimated 11 ribs at the ventrolateral shoulder. The ribs are straight across the inner and middle flank, strengthening, and feebly concave on the outer flank, where they link to feeble inner ventrolateral bullae, from which a strengthening rib links to stronger outer ventrolateral clavi, the ribs linked across the venter by a low, broad, transverse rib, the ventral ribs separated by narrower interspaces. GBA 2016/003/0039 (Text-Figs. 13G, H) is part of one flank and the venter only of a 90° whorl sector with ornament much better-preserved; the maximum preserved whorl height is 32 mm. The flank ornament is comparable to that of the previous specimen. The inner ventrolateral bullae are very feeble, the outer ventrolateral clavi sharp, the venter with a marked siphonal ridge. These specimens compare well with individuals of like size referred to the type species (MATSUMOTO & SARKAR, 1966: Pl. 33, Fig. 1; KENNEDY et al., 2015: Text-Figs. 8a-f). The specimens differ from the smaller specimens referred to Graysonites herein (Pl. 4, Fig. 8), in that their ribs are delicate, crowded, distinctly concave on the outer flank, with very feeble inner ventrolateral bullae.

Occurrence: *Utaturiceras* is restricted to the lower Lower Cenomanian, with records from southern England, south India, Madagascar, KwaZulu-Natal in South Africa, and Nigeria.

Genus Sharpeiceras HYATT, 1903

Type species: *Ammonites laticlavius* SHARPE, 1855: 31, Pl. 14, Fig. 1, by the original designation of HYATT (1903: 111).

Sharpeiceras nigeriense ZABORSKI, 1985

(Pl. 2, Fig. 7; Pl. 3, Figs. 1–4, 7–15; Pl. 4, Figs. 3–5; Text-Fig. 14)

- 1985 Sharpeiceras laticlavium nigeriense ZABORSKI, 26, Text-Figs. 26–28, 31.
- 1987 Sharpeiceras laticlavium nigeriense ZABORSKI, 1985; WRIGHT & KENNEDY: 128, Text-Figs. 32a, b, c, h, i.

Types: The holotype is BMNH C83544, the original of ZA-BORSKI, 1985: 26, Text-Figs. 27a, b. There are four paratypes, BMNH C83542, C83543, C83545, together with a specimen in the collections of the University of Ilorin, Nigeria. All are from the Lower Cenomanian part of the Odukpani Formation on the Calabar-Akamkpa road, 1.5 km north of the junction with the Calabar-Ikot Ekpene road, in Cross River State, Nigeria.

Material: GBA 2016/003/0040-0046, and 25 additional fragments.

Description: The earliest growth stages seen are shown by GBA 2016/003/0041-0042 (Pl. 3, Figs. 1, 2, 7-11). Coiling is involute, the umbilicus comprising 20 % of the diameter, of moderate depth, the umbilical wall flattened and subvertical, the umbilical shoulder quite narrowly rounded. The intercostal whorl section is depressed rectangular, the flanks flattened and parallel, the umbilical shoulders broadly rounded, the venter very feebly convex. The costal whorl section is depressed polygonal, with the greatest breadth at the inner ventrolateral spines. Six broad, feeble primary ribs per half whorl arise on the umbilical wall, and strengthen into small conical umbilical bullae. These giver rise to one or two narrow, sharp, widely separate ribs, whilst additional ribs intercalate, to give a total of 11-12 ribs at the ventrolateral shoulder, where they link to conical to feebly bullate inner ventrolateral tubercles that become subspinose as diameter increases. A near-transverse rib links to a strong conical outer ventrolateral tubercle that also becomes subspinose as diameter increases. From a diameter of 17–18 mm, the inner flank part of the ribs strengthens, and a mid-lateral bulla appears, and becomes increasingly prominent as size increases (compare Pl. 3, Figs. 10, 13, 14). GBA 2016/003/0043 (Pl. 3, Figs. 3, 4) shows the continuing strengthening of tuberculation to a diameter of 40 mm approximately, and provides a link to the largest specimen seen, GBA 2016/003/0046 (Pl. 4, Figs. 3–5). This worn individual has a maximum preserved diameter of 78 mm approximately, the umbilicus comprising 25 % approximately of the diameter. The whorl section appears to have been slightly compressed. There are an estimated 14 ribs per whorl at the ventrolateral shoulder.

A juvenile suture is shown in Text-Figure 14; E/A is moderately incised, very broad and bifid, A narrow and also bifid.

Discussion: Sharpeiceras nigeriense was regarded as a subspecies of S. laticlavium (SHARPE, 1855) (31, Pl. 14, Fig. 1) (see revision in WRIGHT & KENNEDY, 1987: 127, Pl. 41, Fig. 4, Text-Figs. 29, 30, 34a). The holotype of laticlavium is a much larger phragmocone, with a whorl breadth to height ratio of 0.83 at a diameter of 135 mm, the umbilicus comprising 34.5 % of the diameter with 36 primary ribs per whorl. The earliest whorls, at the same diameter as the holotype of nigeriense are not known; the largest paratype of nigeriense (ZABORSKI, 1985: Text-Fig. 26) has ribs that arise in pairs and intercalate, as distinct from the equal, exclusively primary ribs of *laticlavium* at the same diameter. The early growth stage of *nigeriense*, lacking a lateral tubercle is also seen in Sharpeiceras falloti (COLLIGNON, 1931) (10, Pl. 8 (4), Figs. 11, 12, non 9, 10), but at this growth stage coiling is very evolute in falloti, near serpenticone, with a lower expansion rate, the whorls compressed, with the lateral tubercle, when it does appear, very strong (KENNEDY et al., 2015: 12, Text-Figs. 13a-e; 14a-v). Sharpeiceras minor KEN-NEDY et al. (2015: 13, Text-Figs. 12a-i, I-o, 13j-m, 15a-I, 16a-e, 17a-e, 18), from the Lower Cenomanian of northern KwaZulu-Natal in South Africa, is a diminutive species with macroconchs reaching only 63 mm in diameter, the ribs coarser and of lower density than in the present species, the inner, conical ventrolateral tubercles stronger than the outer ventrolateral clavi.

Nuclei of *S. nigeriense* prior to the appearance of the lateral tubercle bear a superficial resemblance to juvenile *Acompsoceras calabarense* ZABORSKI, 1985. They differ in that the umbilical bullae of *calabarense* are coarser, as are the inner



Text-Fig. 14. Partial external suture of *Sharpeiceras nigeriense* ZABORSKI, 1985, GBA 2016/003/0041. flank ribs, which flex back on the outer flank, the inner ventrolateral tubercles are weak, not becoming subspinose, whilst the outer ventrolateral tubercles are clavate rather than conical, do not become subspinose, and there is a blunt siphonal ridge, strengthened into incipient siphonal clavi (compare Pl. 2, Fig. 7; Pl. 3, Figs. 1, 2, 7–11 and Pl. 2, Figs. 3, 4, 8, 9).

Occurrence: Lower Cenomanian of south-eastern Nigeria.

Sharpeiceras florencae SPATH, 1925

(Text-Fig. 15)

- 1925 Sharpeiceras florencae SPATH: 198, PI. 37.
- 2015 *Sharpeiceras florencae* SPATH, 1925; KENNEDY et al.: 14, Text-Figs. 7g–j, p, q, u, v, w; 12j, k, p, q; 16f–h;17f–l, 19–21, 22c–e (with full synonymy).

Type: The holotype, by monotypy, is the original of SPATH (1925: 19, PI. 37) in the collections of the Ditsong Museum of Natural History (formerly the Transvaal Museum), Pretoria, and from northeastern KwaZulu-Natal [Maputoland] in South Africa.

Material: GBA 2016/003/0047 and 0048, from the Lower Cenomanian part of the Odukpani Formation sample 77/50, an outcrop of about 2 m of hard grey marls in a depression on the eastern side of the main road 900 m north of Odukpani village (Text-Fig. 15).

Description: GBA 2016/003/0047 is a crushed 90° whorl fragment with a maximum preserved whorl height of 54 mm. There are parts of six very coarse straight, prorsiradiate ribs on the fragment. They arise on the umbilical wall, and strengthen into coarse umbilical bullae. There are strong lateral bullae, much stronger conical inner ventro-lateral tubercles, and strong outer ventrolateral clavi. The





Sharpelceras florencae SPATH, 1925. GBA 2016/003/0047, the Lower Cenomanian part of the Odukpani Formation at the 77/50 locality (Text-Fig. 1). Figures are natural size.

umbilical wall is marked by a series of depressions to accommodate the inner ventrolateral tubercles of the preceding whorl.

GBA 2016/003/0047 (Text-Fig. 15) is a 60° whorl sector of the phragmocone of a massive shell. The maximum preserved whorl height is 87 mm. The intercostal whorl section is compressed, with a whorl breadth to height ratio of 0.82, the maximum breadth below mid-flank, the flanks feebly convex, the ventrolateral shoulders broadly rounded, the venter very broad, and very feebly convex. The costal whorl section is as wide as high, polygonal, with the greatest breadth at the ventrolateral horns. The umbilicus is quite deep, the umbilical wall feebly convex. Broad ribs arise at the umbilical seam, and strengthen across the wall to develop into strong umbilical bullae. Single strong, straight, prorsiradiate ribs link to a much stronger mid-lateral bulla, linked by a stronger rib to a laterally compressed ventrolateral horn that has developed by the fusion of inner and outer ventrolateral tubercles, such that only a weakened remnant of the inner ventrolateral is present at the inner end of the horn. The costal profile is concave over the mid-ventral region, the ventral rib connecting the horns on opposite flanks effaced.

Discussion: The change in ornament, notably the change in spacing of the ribs between the two fragments is exactly that shown by the holotype, which is 220 mm approximately in diameter. The differences between the present species and others referred to the genus, is discussed at length by KENNEDY et al. (2015: 15).

Occurrence: Lower Cenomanian of northern KwaZulu-Natal in South Africa, Madagascar, Angola, Nigeria, Peru, and northern Mexico.

Subfamily Acanthoceratinae DE GROSSOUVRE, 1894

Genus Acompsoceras HYATT, 1903

Type species: *Ammonites bochumensis* SCHLÜTER, 1871: 1, Pl. 1, Figs. 1–4, by original designation by HYATT, 1903: 111 = *Ammonites renevieri* SHARPE, 1857: 44, Pl. 20, Fig. 2.

Acompsoceras calabarense ZABORSKI, 1985

(Pl. 2, Figs. 3–6, 8, 9, 11–13; Pl. 3, Figs. 5, 6, 16–19; Pl. 5, Figs. 1–13; Text-Fig. 16)

1985 Acompsoceras calabarense ZABORSKI: 29, Text-Figs. 30, 32.

Type: The holotype is BMNH C85250, the original of ZA-BORSKI (1985: 28, Text-Figs. 30, 32); paratypes are BMNH C83552–3, C85249, C85251, from the Lower Cenomanian part of the Odukpani Formation in a cutting on the Calabar–Akamkpa road, 1.5 km north of the junction with the Calabar–Ekpene road in Cross River State, Nigeria.

Material: GBA 2016/003/0048–0055, and 11 additional specimens. GBA 2016/003/0056–0063, from the Lower Cenomanian part of the Odukpani Formation sample 77/50, an outcrop of about 2 m of hard grey marls in a de-



Text-Fig. 16.

External sutures of *Acompsoceras calabarense* ZABORSKI, 1985; A (top): GBA 2016/003/0052; B (bottom): GBA 2016/003/0051.

pression on the eastern side of the main road 900 m north of Odukpani village (Text-Fig. 1).

Description: The earliest growth stages are shown by GBA 2016/003/0048 and 0050 (Pl. 2, Figs. 3, 4, 8, 9). These specimens are up to 15.6 mm in diameter. Coiling is involute, the umbilicus comprising 18 % of the diameter, of moderate depth, with a flattened, outward-inclined umbilical wall. The whorl section is compressed, with a whorl breadth to height ratio of 0.75, the flanks flattened and subparallel, the ventrolateral shoulders broadly rounded, the venter very feebly convex, with a blunt siphonal ridge. There are five to six umbilical bullae of variable strength per half whorl. They give rise to ribs singly or in pairs, the ribs blunt, straight and prorsirsdiate on the inner flank, with some showing a slight backwards flexure on the outer flank, where occasional additional ribs intercalate, to give a total of nine ribs per half whorl at the ventrolateral shoulder, where all link to a small conical inner ventrolateral tubercle, linked by a broad, feebly prorsiradiate rib to a slightly stronger outer ventrolateral clavus. The siphonal ridge is feebly strengthened into incipient clavi in places. GBA 2016/003/0049 (Pl. 2, Figs. 5, 6) is a larger fragment, with a maximum preserved whorl height of 10.5 mm, showing variation in the umbilical bullae from strong to near-effaced, the ribs associated with the stronger bullae weakened and flexed back on the outer flank. The differentiation of the siphonal clavi is better developed than in the previous specimens.

GBA 2016/003/0051–0054 (Pl. 2, Figs. 11–13; Pl. 3, Figs. 5, 6, 16–19) are up to 35 mm in diameter. Coiling remains very involute, with whorl breadth to height ratios of around 0.6, the inner flanks feebly convex and subparallel, the outer flanks flattened and convergent, the ventrolateral shoulders broadly rounded, and the venter very feebly convex, with the feeblest broad siphonal elevation

in some but not all. There are five to six umbilical bullae per half whorl, and 13-14 ribs at the ventrolateral shoulder. The strength of the umbilical bullae remains variable, the ribs arising from them either singly or in pairs, with occasional ribs intercalating. The backwards flexure of some of the stronger, bullate primary ribs is well developed in some (GBA 2016/003/0054: Pl. 3, Figs. 6, 16). The inner ventrolateral tubercle are bullate, the outer ventrolateral clavate in these specimens. Adult body chambers (PI. 5, Figs. 1-13) are up to 112 mm in diameter, and show a range of morphological variation. GBA 2016/003/0060 (PI. 5, Figs. 9, 10) extends to 180°, and appears to be nearcomplete. The intercostal section is compressed, with feebly convex inner, and flattened, convergent outer flanks, the ventrolateral shoulders broadly rounded, the venter feebly convex. At the adapical end, coarse, widely separated umbilicolateral bullae give rise to a strong prorsiradiate rib, with a second rib weakly attached in one case. There are also single intercalated ribs, all of the ribs linking to strong, inner ventrolateral tubercles, beyond which the venter is worn. Towards the adapertural end, the bullae and flank ribs weaken and efface. Specimens such as GBA 2016/003/0057 (Pl. 5, Figs. 7, 8) have the ventral region well-preserved, with conical inner, and clavate outer ventrolateral tubercles. GBA 2016/003/0057 (Pl. 5, Figs. 3, 4) shows the outer ventrolateral clavi weakening at the adapertural end, the inner ventrolateral tubercles weakening and changing to a blunt thickening of the ventrolateral part of the ribs, which are low, broad and flat over the venter. A number of specimens show the sutures (Text-Fig. 16); E/A and A/U₂ are only moderately incised and bifid, as are A and U_2 .

Discussion: The small adult size and very coarse ribs and tubercles, persisting onto the adult body chamber, distinguish this species from others referred to the genus, as comprehensively discussed by ZABORSKI (1985: 29).

Occurrence: Lower Cenomanian of Cross River State, Nigeria.

Acompsoceras sp. juv.

(Pl. 2, Figs. 1, 2, 10)

Material: GBA 2016/003/0064 and 0065.

Description: GBA 2016/003/0064 (Pl. 2, Figs. 1, 2) is a pyritic nucleus 18 mm in diameter. Coiling is very involute, with a tiny, shallow umbilicus, the low wall flattened, the umbilical shoulder broadly rounded. The whorl section is compressed, with a whorl breadth to height ratio of 0.67, the flanks flat and subparallel, the ventrolateral shoulders broadly rounded, the narrow venter very feebly convex, with a low, blunt median ridge. Six low, coarse ribs arise on the umbilical wall, and strengthen into small bullae of variable strength. These give rise to one or two ribs, with additional ribs intercalating, to give a total of 13 to14 ribs at the ventrolateral shoulder. The ribs strengthen markedly on the outer flank and ventrolateral shoulder and link to small conical inner ventrolateral tubercles, linked in turn by a prorsiradiate rib to slightly larger outer ventrolateral clavi. The siphonal ridge is undulose, and strengthened into feeble clavi that are aligned with the outer ventrolateral rows. GBA 2016/003/0065 (Pl. 2, Fig. 10) is a larger fragment, with a maximum preserved whorl height of 14 mm. The adapertural 120° sector is body chamber. Four feeble umbilical bullae are preserved on the fragment. They give rise to single feeble, straight, prorsiradiate ribs with a second rib feebly linked in some cases, together with single intercalated ribs to give a total of 10 ribs at the ventrolateral shoulder. The ribs bear tiny conical inner ventrolateral tubercles and stronger outer ventrolateral clavi. The venter is poorly preserved.

Discussion: These specimens are referred to *Acompsoceras* on the basis of the presence of a siphonal ridge with feeble siphonal clavi in the smalller specimen. They differ from *Acompsoceras calabarense* of the same size in their greater compression, and much higher rib density (compare Pl. 2, Figs. 1, 2, 10; Pl. 2, Figs. 8, 12).

Occurrence: As for material.

Suborder Ancyloceratina WIEDMANN, 1966 Superfamily Turrilitoidea GILL, 1871 Family Turrilitidae GILL, 1871 Genus and subgenus *Mariella* NOWAK, 1916

Type species: *Turrilites bergeri* BRONGNIART, 1822 (395, Pl. 7, Fig. 3), by the original designation of NOWAK (1916: 10).

Mariella (Mariella) bicarinata (KNER, 1852)

(Pl. 6, Figs. 10, 11)

- 1852 *Turrilites bicarinatus* KNER: 9, Pl. 1, Fig. 14, 14a, ? non 14b.
- 2015 Mesoturrilites (Klingerella) bicarinata (KNER, 1852); KLEIN: 173, 174 (with synonymy).

Types: The lectotype, by the subsequent designation of ATABEKIAN (1985: 40) is the original of KNER (1852: Pl. 9, Figs. 14, 14a) from "Mikalince und Czartorya" in what is now Ukraine. The figures were reproduced by WRIGHT & KENNEDY (1996: Text-Figs. 135a, b).

Material: GBA 2016/003/0066-0067.

Description: The fragments consist of a half a whorl only. The maximum preserved whorl height 14.5 mm. The upper whorl face is feebly concave, with shallow radial grooves to accommodate the ribs on the base of the previous whorl. The narrowly rounded junction between upper and outer whorl faces is crenulated, the crenulations corresponding to depressions that housed the lowest row of tubercles on the preceding whorl. The outer whorl face has a feebly convex upper part, the remainder flattened. The lower whorl face is very feebly convex. There are an estimated 10 rows of tubercles per half whorl. The tubercles of the upper row are rounded-conical, and linked to the junction of the outer and upper whorl faces by a low, broad rib. A second row of tubercles is situated on the lower part of the outer whorl face. A third row of much smaller, spirally elongated tubercles lies at the junction of outer and lower whorl faces, sited on a low protuberance that supports a fourth row of very feeble rounded to feebly spirally elongated tubercles. The protuberance gives rise to a low, broad, radial rib on the lower whorl face that effaces progressively across the face.

Discussion: The diagnostic features of *Mariella* (*M*.) *bicarinata* is the conical shape of the tubercles in the upper row, the spiral elongation of the tubercles in the lower rows, and the close juxtaposition of the third and fourth rows of tubercles. Of other species in the Mfamosing fauna, *M.* (*M.*) *essenensis* (GEINITZ, 1849) (PI. 6, Fig. 8) has only three rows of tubercles. *M.* (*M.*) aff. *miliaris* (PICTET & CAMPICHE, 1861) has many more and finer tubercles per whorl, with a well-developed narrow rib linking the upper row of tubercles to the junction of outer and upper whorl surfaces (PI. 6, Figs. 15, 16, 18).

Occurrence: Lower Lower Cenomanian of southern England, Poland, Turkmenistan, and Nigeria.

Mariella (Mariella) essenensis (GEINITZ, 1849) (Pl. 6, Fig. 8)

1849 Turrilites essenensis GEINITZ: 122, Pl. 6, Figs. 1, 2.

2015 *Mariella essenensis* (GEINITZ, 1849); KLEIN: 132, 143 (with synonymy).

Material: GBA 2016/003/0068.

Description: The specimen consists of one and a half whorls, apparently body chamber, with a maximum preserved whorl height of 10 mm. The upper whorl face is concave, the narrowly rounded junction of the upper and outer whorl faces strongly crenulated to accommodate the lowest row of tubercles. The upper part of the outer whorl face is feebly convex, the remainder flattened. There are 15 rows of tubercles per whorl. Those in the upper row are conical. Those in the second row are displaced adaperturally of those in the upper row, only slightly smaller, and spirally elongate. The tubercles in the third row are displaced adaperturally of those in the second row, and conical, lying at the junction of outer and lower whorl faces. They give rise to a coarse radial rib that extends across all of the lower whorl face.

Discussion: The specimen is assigned to *Mariella* (*M.*) *essenensis* on the basis of the presence of only three rows of tubercles, which distinguishes in from other *Mariella* in the present fauna. Of previously described specimens that have been referred to the species, it most closely resembles the original of ATABEKIAN (1985: PI. 10, Fig. 12).

Occurrence: Lower Cenomanian, Southern England, northern France, Germany, Poland, Romania, Iran, Turk-menistan, Mozambique (?), Madagascar, and Nigeria.

Mariella (Mariella) oehlerti oehlerti (PERVINQUIÈRE, 1910) (Pl. 6, Fig. 17)

- 1910 *Turrilites oehlerti* PERVINQUIÈRE: 53, Pl. 14 (5), Figs. 14– 17.
- 2015 *Cenomariella oehlerti oehlerti* (PERVINQUIÈRE, 1910); KLEIN: 152, 154 (with synonymy).

Type: The holotype, by original designation is MNHN. F. J13735, the original of PERVINQUIÈRE (1910: Pl. 14, Fig. 16), from Sour El-Ghoslane (formerly Aumale), Algeria. It was refigured by WRIGHT & KENNEDY (1996: Text-Fig. 138j).

Material: GBA 2016/003/0069–0070, 0076, and six additional specimens.

Description: GBA 2016/003/0069 (Pl. 6, Fig. 17) is a fragment of parts of four successive whorls, with a maximum preserved whorl height of 14 mm. Only the largest whorl preserves all of the ornament. The upper part of the outer whorl face is feebly convex, the remainder flattened. There are four rows of tubercles, the tubercles in successive rows displaced slightly adaperturaly of those in the preceding rows. The conical tubercles in the upper row are the largest, and are borne at the end of a short rib that extends across the upper part of the outer whorl face; there are three in a distance equal to the whorl height. The tubercles of the second row are only slightly smaller, and conical to feebly spirally elongated. The tubercles of the third row are weaker and distinctly spirally elongated, and lie at the base of the outer, exposed whorl face. The tubercles of the fourth row are smaller than those in the third row, spirally elongated, and lie at the junction of the outer and lower whorl faces. They give rise to a low radial rib that effaces across the lower whorl face.

GBA 2016/003/0076 is the largest well-preserved specimen in the present material, with a whorl height of 17 mm, and 25–26 ribs per whorl.

Discussion: The present specimens are referred to *Mariella* (*M.*) *oehlerti oehlerti* on the basis of the subequal conical tubercles in the upper two rows, and the smaller, spirally elongated tubercles in the lower two rows. These features distinguish the species from others in the Mfamosing fauna. *Mariella* (*M.*) *oehlerti sulcata* KLINGER & KENNEDY, 1978 (33, PI. 3, Fig. d; PI. 8, Fig. d; PI. 8, Fig. d; Text-Figs. 3d, e; 8h) differs from the nominate subspecies in having a distinctive spiral groove between the second and third rows of tubercles.

Occurrence: Lower Lower Cenomanian, Algeria, Central Tunisia, Nigeria, KwaZulu-Natal in South Africa, Madagascar, Angola, Japan, and, possibly, northern Mexico.

Mariella (Mariella) aff. miliaris (PICTET & CAMPICHE, 1861)

(Pl. 6, Figs. 15, 16, 18)

Compare:

- 1861 *Turrilites bergeri* BRONGNIART, var. *miliaris* PICTET & CAM-PICHE: 136, PI. 58, Fig. 5.
- 2015 Mariella (Mariella) miliaris (PICTET & CAMPICHE, 1861); KLEIN: 132, 146 (with synonymy).

Type: The holotype, by monotypy, is no. 40041 in the collections of the Musée Geologique, Lausanne, the original of PICTET & CAMPICHE (1861: 136, PI. 58, Fig. 5), from the condensed Upper Albian of Saint Croix, Kanton Waadt, Switzerland. It was refigured by RENZ (1968: PI. 18, Fig. 10).

Material: GBA 2016/003/0071-0074.

Description: GBA 2016/003/0072 (Pl. 6, Fig. 16) is a fragment of two successive whorls, the maximum preserved whorl height 15 mm approximately. The upper part of the outer, exposed whorl face is feebly convex, the remainder flattened. Weak ribs arise at the junction of upper and outer whorl faces: there are five to six ribs in a distance equal to the whorl height. The ribs are very feebly prorsiradiate and have the same width as the interspaces. They strengthen across the whorl face, and link to small, transversely elongated tubercles just above the mid-point of the face. A relatively wide, near-smooth zone is crossed by the feeblest of ribs, arising from the tubercles of the first row, developing into a barely detectable swelling at the midpoint between the first row and the second row of welldeveloped, transversely elongated tubercles. A well-developed rib extends to a third row of tubercles at the junction of outer and lower whorl faces. These tubercles give rise to a relatively coarse rib that extends across the lower whorl face. GBA 2016/003/0074 (Pl. 6, Fig. 18) consists of three successive whorls. The greatest measurable whorl height is 14 mm approximately. The density and strength of the ribbing and tuberculation is as in the previous specimen, but here the second row of tubercles is well developed. There are 27-28 ribs per whorl.

GBA 2016/003/0071 (PI. 6, Fig. 15) consists of a half whorl with a maximum preserved whorl height of 14 mm. There are five ribs in a distance equal to the whorl height, slightly prorsirsdiate, and linking to a well developed transversely elongated tubercle a little above the mid-point of the outer, exposed whorl face. These are separated by a narrow, near-smooth zone from a second row of conical to feebly transversely elongated tubercles, linked by a blunt rib to a close-spaced third and fourth rows of smaller tubercles, the fourth row at the junction of outer and lower whorl faces, and giving rise to a coarse radial rib that weakens progressively across the lower and inner whorl faces.

Discussion: These specimens are linked together by the well-developed tuberculate rib on the upper part of the outer whorl face and the succeeding near-smooth zone where the ribs near-efface. GBA 2016/003/0074 (PI. 6, Fig. 18) appears to have only three rows tubercles, but this is interpreted as a pathological condition, the fourth row represented by a very weak development in the nearsmooth zone below the first row. The well developed rib on the upper part of the outer whorl face distinguishes these specimens from the other Mariella recognized in the Mfamosing fauna. The qualified determination given here is based on the rib density of the present material, 27-28 per whorl, substantially lower than that of the holotype of *mili*aris, where they number 54 per whorl. Lower rib densities of 25-35 are seen in specimens from the Upper Albian of Turkmenistan assigned to miliaris by ATABEKIAN (1985: 29, Pl. 6, Figs. 1–3; Pl. 5, Figs. 5–12).

Occurrence: As for material. *Mariella (M.) miliaris* is typically an Upper Albian species, with records from southern and eastern England, France, Switzerland, Hungary, Romania, Sardinia, Turkmenistan, and KwaZulu-Natal in South Africa. There are Lower Cenomanian records from Mozambique and southern England.

Mariella (Mariella) cenomanensis (SCHLÜTER, 1876) (Pl. 6, Fig. 6)

- 1876 Turrilites cenomanensis SCHLÜTER: 131, Pl. 37, Figs. 6–8.
- 2015 *Mariella cenomanensis* (SCHLÜTER, 1876); KLEIN: 132, 139 (with synonymy).

Type: The lectotype, by the subsequent designation of KENNEDY (1971: 29), is the original of SCHLÜTER (1876: 131, Pl. 37, Fig. 6), allegedly no. 74 in the collections of the Paläontologisches Institut of Bonn University, and from the rotomagensis-Pläner of Lichtenau, Westphalia. It was figured by WRIGHT & KENNEDY (1996: Text-Fig. 141b); the specimen bears little relationship to Schlüter's illustration, while the horizon of the lectotype is Lower Cenomanian (KAPLAN et al., 1998: 208).

Material: GBA 2016/003/0075.

Description: The specimen consists of two whorls; the greatest preserved whorl height is 10 mm approximately. The junction between upper and outer whorl faces is markedly crenulated to accommodate the lowest row of tubercles of the previous whorl. 17 to 18 strong ribs per whorl arise at the junction of the upper and outer whorl faces, and are feebly prorsiradiate, linking to a transversely elongated tubercle above the mid-point of the outer whorl face. A smooth zone separates this row of tubercles from a second row of smaller adaperturally displaced conical tubercles, with a third row, adaperturally displaced and just above the inter-whorl suture. A fourth row of much smaller tubercles is situated on the outermost part of the lower whorl face. They give rise to well-developed radial ribs on the lower whorl face.

Discussion: This specimen differs from other *Mariella* in the present collection in having coarse ribs and stronger tubercles in the upper row. It compares closely with *Mariella* of comparable size from southern England that were referred to *cenomanensis* by WRIGHT & KENNEDY (1996: PI. 100, Fig. 11).

Occurrence: Lower Cenomanian, Germany, France, southern England, Poland, Romania, northeastern Russia, Turkmenistan, Kazakhstan, Iran, Algeria, Nigeria, and Madagascar.

Genus Hypoturrilites DUBOURDIEU, 1953

Type species: *Turrilites gravesianus* D'ORBIGNY, 1842: 596, Pl. 144, Figs. 3–5, by original designation by DUBOURDIEU (1953: 123).

Hypoturrilites betaitraensis COLLIGNON, 1964

(Pl. 6, Figs. 1–5, 7, 9, 12–14)

- 1964 *Hypoturrilites betaitraensis* COLLIGNON: 13, PI. 320, Figs. 1837–1838.
- 2015 *Hypoturrilites betaitraensis* COLLIGNON, 1964; KLEIN: 156, 158 (with synonymy).

Type: The holotype, by original designation is the original of COLLIGNON (1964: 13, PI. 320, Fig. 1387) from the Lower

Cenomanian of the 'Vallée de la Betaitra, Fontaine Tunisienne', Madagascar. It was refigured by WRIGHT & KENNEDY (1996: Text-Fig. 134f).

Material: GBA 2016/003/0077-0086, plus nine additional fragments.

Description: Fragments comprise up to three whorls, with whorl heights of up to 13 mm. The upper whorl face is concave, with radial grooves to accommodate the ribs on the base of the previous whorl. The junction between upper and outer whorl faces is markedly crenulated to accommodate the lowest row of tubercles of the previous whorl. The outer whorl face is feebly convex. There are four rows of tubercles. Those in the upper row are the largest and number six per half whorl. They are conical, and positioned on the upper part of the face, and are linked to the junction of the outer and upper whorl faces by one or two variably developed ribs (PI. 6, Fig. 2), with a single weak rib intercalating between successive tubercles (Pl. 6, Figs. 13, 14). The second row of conical tubercles are smaller than those in the upper row, are displaced adaperturally, and twice as numerous, corresponding to the tubercles and intercalated ribs in the upper row. The tubercles of the third row lie at the junction of the outer and lower whorl faces, and are feebly spirally elongated. The tubercles of the fourth row are situated on the outer part of the lower whorl face, close to those of the third row, and give rise to blunt radial ribs that efface across the lower whorl face.

GBA 2016/003/0081 (PI. 6, Fig. 7) has ornament of this type on the penultimate whorl. On the final whorl, the differentiation of tubercles and intercalated ribs in the upper row is lost, being replaced by equal ribs that extend across the upper part of the outer whorl face, strengthening into weak transversely elongated tubercles at their lower end. The tubercles of the second row are also transversely elongated.

Discussion: The ribs linking the upper row of tubercles to the junction between outer and upper whorl faces, with ribs between the tubercles, is immediately distinctive. A combination of ribs and tubercles is also seen in species known only from much larger specimens. Of these, Hypoturrilites laevigatus (COQUAND, 1862: 175, Pl. 2, Fig. 6) (of which Turrilites tenouklensis PERVINQUIÈRE, 1910: 57, PI, 14 (5). Fig. 31 is a synonym) is revised by WRIGHT & KENNEDY (1996: 373, Pl. 102, Fig. 2; Text-Figs. 146k-m, p, q) and KENNEDY in KENNEDY & GALE (2015: 312, Pl. 24, Fig. 18; Text-Figs. 34a-d), has many more and finer ribs on the outer whorl face, and only three rows of tubercles. Hypoturrilites tuberculatoplicatus (SEGUENZA, 1882: 115, Pl. 5, Fig. 3 (see revision in WRIGHT & KENNEDY, 1996: 374, Pl. 108, Fig. 7; Pl. 113, Figs. 3, 4, 6, 8, 9) has four rows of tubercles, as in the present species, but the outer whorl face is covered in far more numerous delicate ribs.

The striking changes of ornament between the penultimate and final whorl of GBA 2016/003/0081 (Pl. 6, Fig. 7) are interpreted as those the adult body chamber of a microconch.

Occurrence: Lower Lower Cenomanian where well dated. The geographic distribution extends from Madagascar to KwaZulu-Natal in South Africa, Nigeria, Brazil, Algeria, Turkmenistan, Haute-Savoie in France, and southern England.

Appendix: Macrofossils (excluding ammonites) from the hardground on top of the Mfamosing Limestone

FRANZ STOJASPAL (†)

The hardground faunas include a range of other organisms in addition to the ammonites described above, notably internal moulds of bivalves and gastropods, oysters, *Holaster* sp. and trace fossils: *Lithophaga* borings and *Thalassinoides* burrows. The material is kept in the GBA collections under the acquisition number GBA 1980/004. The following list comes from an internal GBA report by the late Franz Stojaspal:

Bivalves

1980/004/0001	Nuculana (? cf. cultellus KOENEN)
1980/004/0002	Trigonarca cf. diceras (Seguenza)
1980/004/0003	?Phelopteria sp. [specimen missing]
1980/004/0004	Camptonectes cf. cretosus (DEFRANCE)
1980/004/0005	<i>Neithea aequicostata</i> (LAMARCK): world- wide distribution from Albian–Senoni- an
1980/004/0006	Plicatula auressensis Coquand: Upper Al- bian-Senonian of Africa
1980/004/0007	Lima sp.
1980/004/0008	Lopha lombardi DARTEVILLE & FRENEIX: known only from the Santonian–Cam- panian of West Africa
1980/004/0009	<i>Pycnodonta vesicularis</i> (LAMARCK): world- wide distribution from Aptian–Senoni- an
1980/004/0010	Astarte sp.
1980/004/0011	<i>Martesia cylindrica</i> RIEDEL, known only from the Coniacian of Bombe (Cameroon)
1980/004/0012	Goniomya cf. beyrichi CHOFFAT
1980/004/0021	Trigonia crenulata LAMARCK

Gastropods

1980/004/0013	<i>Turritella</i> sp.
1980/004/0014	Nerinea sp.
1980/004/0015	Helicaulax sp.
1980/004/0016	Rostellaria sp.
1980/004/0017	Tylostoma sp.
1980/004/0018	Volutilithes sp.
1980/004/0019	Avellana incrassata (SOWERBY)

Echinoidea

1980/004/0020

Holaster sp.

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Figs. 1–5: Flickia bullata sp. nov.

1, 2: paratype GBA 2016/003/0011; 3-5: the holotype, GBA 2016/003/0010.

Figs. 6-14: Puzosia (Anapuzosia) sp.

6, 7: GBA 2016/003/0016; 8: GBA 2016/003/0014; 9-11: GBA 2016/003/0012; 12: GBA 2016/003/0015; 13: GBA 2016/003/0018; 14: GBA 2016/003/0017.

Figures 1–5, 9–11 are x 2, Figures 6–8, 12–14 are natural size.







Figs. 1, 2, 10: Acompsoceras sp. juv.

1, 2: GBA 2016/003/0064; 10: GBA 2016/003/0065.

Figs. 3–6, 8, 9, 11–13: Acompsoceras calabarense ZABORSKI, 1985.

3, 4: GBA 2016/003/0048; 5, 6: GBA 2016/003/0049; 8, 9: GBA 2016/003/0050; 11: GBA 2016/003/0051; 12, 13: GBA 2016/003/0052.

Fig. 7: Sharpeiceras nigeriense ZABORSKI, 1985, GBA 2016/003/0040.

Figs. 14-22: Salaziceras nigerianum FÖRSTER & SCHOLZ, 1979.

14: GBA 2016/003/0027; 15, 16: GBA 2016/003/0028; 17, 18: GBA 2016/003/0029; 19, 20: GBA 2016/003/0030; 21, 22: GBA 2016/003/0031.

All Figures are x 2.















Figs. 1–4, 7–15: Sharpeiceras nigeriense ZABORSKI, 1985.

1, 7–9: GBA 2016/003/0041; 2, 10, 11: GBA 2016/003/0042; 3, 4: GBA 2016/003/0043; 12, 13: GBA 2016/003/0044; 14, 15: GBA 2016/003/0045.

Figs. 5, 6, 16–19: Acompsoceras calabarense ZABORSKI, 1985.

5, 18, 19: GBA 2016/003/0053; 6, 16, 17: GBA 2016/003/0054.

Figures 1–6 are natural size, Figures 7–19 are x 2.



















Figs. 1, 2, 6-8: Graysonites wacoense (BÖSE, 1928).

1, 2: GBA 2016/003/0037; 6, 7: GBA 2016/003/0036; 8: GBA 2016/003/0035.

Figs. 3–5: Sharpeiceras nigeriense ZABORSKI, 1985, GBA 2016/003/0046.

All Figures are natural size.



Figs. 1–13: Acompsoceras calabarense ZABORSKI, 1985.

1, 2: GBA 2016/003/0056; 3, 4: GBA 2016/003/0057; 5, 6: GBA 2016/003/0058; 7, 8: GBA 2016/003/0059;

9, 10: GBA 2016/003/0060; 11: GBA 2016/003/0055; 12, 13: GBA 2016/003/0061.

The originals of Figures 1–8, 9–13 are from the Lower Cenomanian part of the Odukpani Formation at locality 77/50, North of Odukpani; the original of Figure 11 is from the Mfamosing Quarry.

All Figures are natural size.



Figs. 1–5, 7, 9, 12–14: *Hypoturrilites betaitraensis* (COLLIGNON, 1964).

1: GBA 2016/003/0083; 2: GBA 2016/003/0077; 3: GBA 2016/003/0078; 4: GBA 2016/003/0079; 5: GBA 2016/003/0080;

7: GBA 2016/003/0081; 9: GBA 2016/003/0082; 12: GBA 2016/003/0084; 13: GBA 2016/003/0085; 14: GBA 2016/003/0086.

All of these figures are natural size.

Fig. 6: Mariella (Mariella) cenomanensis (SCHLÜTER, 1876), GBA 2016/003/0075.

Fig. 8: Mariella (Mariella) essenensis (GEINTZ, 1849), GBA 2016/003/0068.

Figs. 10, 11: Mariella (Mariella) bicarinata (KNER, 1852).

10: GBA 2016/003/0066; 11: GBA 2016/003/0067.

Figs. 15, 16, 18: *Mariella* (*Mariella*) aff. *miliaris* (PICTET & CAMPICHE, 1861). 15: GBA 2016/003/0071; 16: GBA 2016/003/0072; 18: GBA 2016/003/0074.

Fig. 17: Mariella (Mariella) oehlerti oehlerti (PERVINQUIÈRE, 1910), GBA 2016/003/0069.

All of these figures are x 2.

