The Ammonite Genera *Oxydiscites* DACQUÉ 1934 and *Sphaerodomites* ROLLIER 1909 (Strigoceratidae, Middle – Late Jurassic)

GÜNTER SCHWEIGERT, STUTTGART, FRANÇOIS ATROPS, LYON; ATILIO BENETTI, VELO VERONESE & ARNOLD ZEISS, ERLANGEN

Abstract

A revision of the ammonite genus *Oxydiscites* DACQUÉ 1934 and its microconch counterpart *Sphaerodomites* ROLLIER 1909 is presented. The lineage of these dimorphic genera goes back to the Late Callovian with the hitherto stratigraphically oldest known species *Oxydiscites margaritatus* (CARKXI & SEQUEIROG) (syn.: *Securisites securicristatus* CARKXI, ELMI & MANGOLD) and *Oxydiscites multiformis* (de GROSSOUVR) both from the base of the Athleta Zone. The new species *Oxydiscites geyeri* n. sp. is described from the Transversarium Zone of Sicily. A very well preserved specimen of the microconch ammonite species *Sphaerodomites ebeli* (SCHWEIGERT), originally only known by the holotype is reported from the Platynota Zone of the Venetian Alps. The morphological features of this specimen gives reason to take the genus *Barthelia* OLÉRIZ & SCHÄRER 1983 as a junior synonym of *Sphaerodomites* ROLLIER 1909. *O. ellypticus* (OLÉRIZ) hitherto only known from Southern Spain and the Pre-Rif mountains of Morocco is the youngest known chronospecies of *Oxydiscites*; it comes from the Hypselocyclum Zone.

Some sculptural characters which have been overlooked in earlier investigations and the dimorphism itself indicate a derivation of *Oxydiscites/Sphaerodomites* from the Phlycticeras lineage of the Strigoceratidae, most probably via the Middle Bathonian genus *Strungia* ARKELL.

Zusammenfassung


Einige skulpturale Merkmale, die bisher übersehen worden waren und auch der eigen tümliche Dimorphismus selbst zeigen, daß diese Ammonitengruppe offensichtlich zu der Phlycticeratiden-Linie der Strigoceratidae gehört und sich höchstwahrscheinlich über die mittelbalearische Gattung *Strungia* ARKELL ableiten läßt.

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1 INTRODUCTION

Recently, the Upper Jurassic ammonite genus Oxydiscites was recognized to represent the dimorphic counterpart ("antidimorph") of the very rare genus Barthelia (Schweigert 1985). At that time, the microconch genus Barthelia was known by only three specimens from Spain and a further specimen from Southern Germany; another figured specimen probably belonging to Barthelia from Southern Germany was lost in the collection. A well preserved specimen of Barthelia ebela Schweigert from a neptunian dyke of the Lessini Mountains (N Italy) initiated further research on the systematics of this enigmatic ammonite group. The results of these new investigations are presented herein.

Abbreviations (dimensions in mm):
D = diameter; H = height of last whorl; U = width of umbilicus; W = width of cross section; Z/2 = secondary ribs/half a whorl; [M] = macroconch; [m] = microconch;
SMNS = State Museum of Natural History Stuttgart; GDF = Institute of Geology and Palaeontology, University of Tübingen; CP = Collection of the University of Poitiers;
MFL = Collection of the Museo dei Fossili della Lessinia, Camposilvano, Italy.

2 NEW RESULTS ON OXYDISCITES AND PHYLOGENETIC CONCLUSIONS

When listing the records of Oxydiscites and Barthelia (Schweigert 1995), it was overlooked, that a further specimen of "Barthelia sp." was mentioned from the Southern Alps (Benetti & Pezzana 1988). This specimen, coming from the Bimammatum Zone of the Lessini Mountains (Italy, Prov. Verona), could be determined as Barthelia subbetica Olóriz & Schärer. It was found in approximately the same stratigraphic position as the holotype from Southern Spain. Palaeogeographically this record of Barthelia from Northern Italy is not very surprising, since a macroconch antidimorph, Oxydiscites praesemiformis (Olóriz), has been reported from the Herbichi Zone of the same area (Sann 1993; Schweigert 1995). Later, another specimen of Barthelia was discovered within an ammonite fauna from a neptunian dyke located in the western part of the Lessini Mountains. A part of this fauna was already described by Benetti et al. (1990). The new Barthelia specimen which is described in the systematic chapter below obviously comes from the Platynota Zone and belongs to Barthelia ebela Schweigert, a species previously only known by the holotype from Southern Germany.

From the Late Callovian (Athleta Zone, Trezzense Subzone) of France and Algeria Carou et al. (1992) described ammonites which are strikingly similar to Oxydiscites. However, Carou et al. (1992) concluded that the "Kimmeridgian" genus Oxydiscites is a direct descendant of Ochetoceras splitting off somewhere in the Late Oxfordian. Hence, these authors believed the forms from the Athleta Zone being nothing else but homoeomorphic with Oxydiscites, and therefore they created the new ammonite genus Securisites. The ancestors of Securisites were said to be oppelids like Paralciida. However, when establishing the new genus Securisites, Carou et al. (1992) did not know the adult sculptural stage of Oxydiscites laffoni (Moesch). Apart from an undulating venter in Oxydiscites laffoni, there is in fact no difference in the sculptural features between both genera. Because of the shape of the aperture there is no doubt that all three figured specimens of Securisites from the Athleta Zone represent macroconchs. To us the question arose, if these are really only homoeomorphs or true Oxydiscites. This question can be answered by looking for Barthelia-like microconchs in much older strata than the Late Oxfordian which could represent stratigraphical links to fill the enormous stratigraphical gap between the Late Callovian Athleta Zone and the Late Oxfordian Bimammatum Zone. As a possible candidate we focused on the poorly known genus Sphaerodomites Rollier 1909, which is known from the Cordatum Zone of the Lower Oxfordian. Sphaerodomites was said to differ from Barthelia by its shoal grooves on both sides of the keel. Already Olóriz & Schärer (1983) remarked a close resemblance between Barthelia subbetica and the much older Sphaerodomites calcaratus (Couquand).

If a direct lineage between Sphaerodomites and Barthelia really exists, Sphaerodomites is postulated to occur in the Athleta Zone, and, on the other hand, Oxydiscites in the Cordatum Zone. In the Athleta Zone the presumed macroconchs are also only known by very few specimens, so that there would be no wonder that records of the microconchs are missing yet. Possibly, these missing Sphaerodomites have been figured as "Tarameliaceras taurimontanum (ERNI)" (see Carou & Sequieres 1987, pl. 1, fig. 13), but further studies must be done.

Surprisingly Rollier (1909) mentioned forms related to Oxydiscites when discussing Ammonites laffoni for the first time (see below). The type species of the genus Sphaerodomites, Ammonites calcaratus Couquand, was described by Couquand (1853) together with another ammonite termed as Ammonites pidanceti Couquand. Both ammonites were
figured not only on the same plate, but they both came from the same beds (Cordatum Zone) of the same locality within the present city area of Besançon. There is little doubt that *Ammonites pidanceti* COQUAND was included in *Oxydiscites* already by ROLLIER (1909), although he did not establish this genus correctly according to the ICZN. After the investigation of a topotype and the establishment of this genus correctly according to the ICZN, AMMONITES Pidancreti OF OXYDISCITES becomes evident. However, this species is extremely rare, so that up to the present besides the figured holotype no further specimen of the same size has been reported, and the species has nearly been forgotten or misinterpreted as a taramelliceratid.

The well preserved new finding of *Barthelia ebeli* from Italy features very weak depressions on both sides of the keel, which are not visible in *Barthelia subbetica* because of the poor preservation of all published specimens. In the holotype of *Barthelia ebeli*, the keel is partly also accompanied by weak grooves. The shape of the venter in the holotype of *Sphaerodomites calcaratus* (COQUAND) is in principal very similar to that of *Barthelia ebeli*. It only depends on the stage of preservation (steinkern or shell preservation), if the grooves or depressions are visible or not. It should be noted that the only difference between *Sphaerodomites* and *Barthelia* is nothing but an inconsistent feature depending on the preservation. Hence, there is no reason for a taxonomic separation of both genera from each other, and we treat the genus *Barthelia* OLÖRIZ & SCHAERER now as a junior synonym of *Sphaerodomites ROLLIER*.

The phylogenetic succession of all known chronospecies of the dimorphic couple *Oxydiscites*/*Sphaerodomites* is shown in table 1.

**Table 1. Updated knowledge on the development of the dimorphic couple *Oxydiscites* – *Sphaerodomites*.**

<table>
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<tr>
<th>Age</th>
<th>Oxydiscites [M]</th>
<th>Sphaerodomites [m]</th>
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<tr>
<td>Hypselocyclum Zone</td>
<td><em>O. ellipticus</em></td>
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<td>Spain, Morocco</td>
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<tr>
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<td><em>O. praesemiformis</em></td>
<td>still unknown</td>
<td>Spain, Southern Alps</td>
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<td>Platynota Zone</td>
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<td><em>S. eboli</em></td>
<td>S Germany, Switzerland, SE</td>
</tr>
<tr>
<td>Planula Zone</td>
<td>still unknown</td>
<td><em>S. cf. subbeticus</em></td>
<td>France, S Alps, S Spain</td>
</tr>
<tr>
<td>Bimammatum Zone</td>
<td>still unknown</td>
<td><em>S. subbeticus</em></td>
<td>S Spain</td>
</tr>
<tr>
<td>Bifurcatus Zone</td>
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<td>still unknown</td>
<td>Spain, S Alps, ? S Germany</td>
</tr>
<tr>
<td>Transversarium Zone</td>
<td><em>O. geyeri n. sp.</em></td>
<td>still unknown</td>
<td>still unknown</td>
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<tr>
<td>Cordatum Zone</td>
<td>still unknown</td>
<td><em>S. reynelensis</em></td>
<td>Sicily</td>
</tr>
<tr>
<td>Cordatum Zone</td>
<td><em>O. pidanceti</em></td>
<td><em>S. calcaratus</em></td>
<td>E France</td>
</tr>
<tr>
<td>Mariae Zone</td>
<td><em>O. cf. pidanceti</em></td>
<td>still unknown</td>
<td>Switzerland, France, Syria</td>
</tr>
<tr>
<td>Athleta Zone</td>
<td><em>O. margaritatus</em></td>
<td>&quot;T. taurimontanum&quot;</td>
<td>N France, S England</td>
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<td><em>O. multiformis</em></td>
<td>still unknown</td>
<td>W France, E Spain</td>
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**3 SYSTEMATICS OF THE AMMONITE GENERA OXYDISCITES AND SPHAERODOMITES**

**3.1 The macroconchs: Oxydiscites**

**Family Strigoceratidae BUCKMAN 1924**

**Subfamily Phyltoceratinae SPATH 1925**

**Genus Oxydiscites DACQUÉ, 1934 [M]**

(Synonyms: Metastreblites OLÖRIZ 1978; *Securisikis CARIOU, ELMI & MANGOLD 1992*; *Platynota* SLAUGHTER 1867.);

**Emended Diagnosis:** Oxycone small sized ammonite genus with minute umbilicus and scaphitoid adult stage, finely serrate high septiform keel, inner whorls sphaerocone, falcoid ribbing, aperture with hook-like umbilical thickening, spiral strigation present in well preserved specimens.

**Type species:** Ammonites laffoni MOESCH 1867.

**Remarks.** – The genus *Oxydiscites* was proposed by ROLLIER (1909: 8), based on an ammonite species from the "Argovien inférieur" of the Randen area (NE Switzerland or SW Germany) which he intended to describe in a later paper as *Oxydiscites merkleini* n. sp. The exact finding locality was not mentioned. However, *Oxydiscites merkleini* ROLLIER remained a nomen nudum, because the planned paper has never been published. Hence, nothing is known about the number of specimens in the large collection of ROLLIER, and if these are still available. Nevertheless, when mentioning *O. merkleini*, ROLLIER compared it with *Ammonites laffoni*
MOESCH and Ammonites pidanceti COQUAND assuming that all three are closely related. He also did not designate a type species of the genus Oxydiscites; therefore only the nomen nudum "merkleini" can be assigned to this genus without any doubt. ARKELL (1956: 279) took DACQUE as author of the genus Oxydiscites, who had subsequently designated Ammonites laffoni MOESCH as type species. After GEYER (1960) the genus Oxydiscites was established by DACQE, based on the single species Ammonites laffoni, from which previously only one specimen was known, thus being the holotype by monotypy. GEYER (1960) recorded two further specimens from western Swabia housed in the collections of the SMNS. However, the French text of DACQUE himself, who accepted ROLIER as author of the genus Oxydiscites. We prefer to keep Ammonites laffoni and Ammonites pidanceti within a single genus. An undulation of the venter in the symmetry plane, which occurs in O. laffoni, is obviously not developed in the early forms from the Callovian and the Oxfordian described below.

Oxydiscites margaritatus (CARIOU & SEQUEIROS)

Fig. 1

*1987 Taramellliceras margaritatus n. sp. – CARIOU & SEQUEIROS, p. 500, pl. 1, fig. 5-6.
1992 Securisites securicristatus nov. sp. – CARIOU et al., p. 1269, pl. 1, fig. 1.

Holotype: Specimen figured by CARIOU & SEQUEIROS 1987, pl. 1, fig. 5.
Locus typicus: Montreuil-Bellay, W France.
Stratum typicum: Athleta Zone, Treezense Subzone.

Description: The holotype is an incomplete specimen lacking the main part of the bodychamber, so that only the taramelliteid ribbing stage was recognized, while the succeeding scaphitoid stage is visible in a complete specimen described in detail and figured by CARIOU et al. (1992) (= Holotype of Securisites securicristatus).

Measurements:

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<td>29.2</td>
<td>2.0</td>
<td>20.3</td>
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Fig. 1. Oxydiscites margaritatus (CARIOU & SEQUEIROS). Cast of a new finding. Upper Callovian, Athleta Zone, Treezense Subzone, Montreuil-Bellay, W France. CP, no. MBe 652b (leg. E. CARIOU). a: Ventral views, b: lateral views. – x1.

Fig. 2. Oxydiscites multiformis (DE GROSSOWE), holotype, reproduced from DE GROSSOWE 1891, pl. 9, fig. 1. Upper Callovian, Athleta Zone, Treezense Subzone, Montreuil-Bellay, W France. a: Ventral views, b: lateral view. – x1.

Fig. 3. Oxydiscites pidanceti (COQUAND), holotype, reproduced from COQUAND 1853, pl. 14, fig. 3-4. Lower Oxfordian, Cordatum Zone, Renggeri Clay Formation, Besançon-Palente. a: Lateral view, b: Ventral view. – x1.

Fig. 4. Sphaerodomites calcarius (COQUAND), holotype, reproduced from COQUAND 1853, pl. 14, fig. 7-8. Lower Oxfordian, Cordatum Zone, Renggeri Clay Formation, Besançon-Palente. a: Lateral view, b: Ventral view. – Enlarged.

Fig. 5. Oxydiscites pidanceti (COQUAND), topotype showing the finely serrate keel. Université de Franche-Comté, Besançon (Coll. I. PIDANCET, without no.). a: Lateral view, b: Ventral view. – x1.

Fig. 6. Oxydiscites cf. pidanceti (COQUAND), juvenile specimen. Lower Oxfordian, Marie Zone, Marnes de Villers Formation, Houlgate, N France. SMNS 63820 (leg. A. ILG). a: Lateral view, b: Ventral view. – x2.

Fig. 7. Oxydiscites pidanceti (COQUAND). Lower Oxfordian, Cordatum Zone, Renggeri Clay Formation, Champagnole, Mont Rivel, E France. SMNS 63464/1 (leg. B. HOSTETTLEN). a: Ventral view, b: Lateral view. – x1.

Fig. 8. Oxydiscites geyeri n. sp., holotype. Middle Oxfordian, Transversarium Zone, Rocca Busambra, W Sicily. GPT no. 1855 (leg. J. WENDT). – a: Ventral view, b: Lateral view. – x1.

Fig. 9. Sphaerodomites subbeticus (OLONZ & SCHUERM), cast of the holotype. Upper Oxfordian, Bimammatum Zone, Sierra del Quijar S Cehegin, Province of Murcia, Spain. Universidad de Granada collection. – x1.

Fig. 10. Sphaerodomites ebeti (SCHWEIGERT). Lower Kimmeridgian, Platynota Zone, Neptunian dyke "Ambrosi" near Breonio, W Monti Lessini, Province of Verona, Italy. MFL, no. G.A.1* 52 (leg. A. BENETTI); see Fig. 16. – x1.

Fig. 11. Oxydiscites laffoni (MOESCH). Lower Kimmeridgian, Platynota Zone, Lacunosamerget Formation, Obernheim, SW Germany. SMNS no. 62607 (leg. R. DOPATKA). – x1.
Oxydiscites multiformis (DE GROSSOUVRE)

Fig. 2

1891 Ammonites multiformis. - DE GROSSOUVRE, p. 260, pl. 9, fig. 1.

1911 Petitclercia multiformis. - ROLLIER, p. 311.

1928 Petitclercia multiformis GROSSOUVRE. - SPATH, p. 90.

1936 Petitclercia multiformis DE GROSSOUVRE sp. - GÉRARD & CONTAUT, p. 32.

1992 Securisites aenigmatica n. sp. - CARIOU et al., p. 1269, pl. 1, fig. 2-4.

Holotype: Specimen figured by DE GROSSOUVRE, pl. 9, fig. 1 (monotypical).
Locus typicus: Montreuil-Bellay, Western France.
Stratum typicum: Oolite Ferrugineuse de Montreuil-Bellay, Athleta Zone, Trazense Subzone.
Occurrence: W France, N Africa.

Description. - See CARIOU et al. 1992.

The extremely rare Middle Jurassic ammonite species Ammonites multiformis DE GROSSOUVRE has lately almost been fallen into oblivion, possibly because this species has only been figured once. The holotype is not only identical with Securisites aenigmatica from a morphological point of view, but it comes from the same stratigraphical level. All sculptural elements including the ribs, which end in delicate ventromarginal tubercles are also present in Oxydiscites margaritatus (= S. securicirratus). The latter also comes from the Athleta Zone and even from the same finding locality as Ammonites multiformis, so that both may be interpreted as different morphotypes within the variability of a single biochronospecies. The specific name, however, does not point to this variability, but to the succeeding sculptural stages. The holotype of Ammonites multiformis is a peculiarly large specimen, in which the last sculptural stage is not preserved. In contrast, the stage marked by ventromarginal tubercles is very prominent in that specimen. Thus, it is well comparable with "Oppelia" redlichii from the Bathonian of Romania (POPOVICI-HATZEG 1905, pl. 5, fig. 1), which is the type species of the ammonite genus Strungia ARKELL. Strungia was mentioned from the Bathonian of France and Arabia (ARKELL 1952; ELM 1967), but at least all figured French specimens do certainly not belong to Strungia. Strungia redlichii bears a strigation, which indicates a close relation to the Strigoceratidae. Thus, Strungia redlichii represents both a morphological and stratigraphical link between Phlycticeratinae of the early Bathonian (P. dorsocavatum [QUENSTEDT]) and Oxydiscites multiformis (DE GROSSOUVRE) of the early Late Callovian. On the other hand, already in the late Bajocian some forms occur, which exhibit stronger morphological affinities with Oxydiscites. FERNÁNDEZ LÓPEZ (1985) described them as "Melendezia sp.". The type species of Melendezia, M. aenigmatica FERNÁNDEZ LÓPEZ, which clearly differs from the latter forms, is now included in the genus Phlycticeras (see SCHWEIGERT & DIETZE 1998, 1999).

Measurements:

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Oxydiscites pidanceti (COQUAND)

Fig. 3, 5-7

1853 Ammonites Pidanceti. - COQUAND, p. 440, pl. 14, fig. 3-4.

1866 Ammonites Pidanceti COQUAND. - OPPEL, p. 215.

1900 Oppelia episcopalis, P. DE LORIOL. - LORIOL, p. 41, pl. 3, fig. 21-24, non fig. 17-20.

1928 Tarameliceras kiliani n. sp. - MAIRE, p. 31, pl. 2, fig. 14.

1939 Tarameliceras episcopale (DE LORIOL) var. globosa DE LORIOL. - ARKELL, pl. 8, fig. 6.

1955 Tarameliceras (Proscaphites) globosus (DE LORIOL). - HAAS, p. 102, pl. 16, fig. 26-27.

Holotype: Specimen figured by COQUAND 1853, pl. 14, fig. 3-4.
Locus typicus: The locality "Palente" is situated within the town of Besançon (pers. comm. A. BOULLIER-ROLLET, Besançon).
Stratum typicum: Lower Oxfordium, Cordatum Zone (cf-specimens from the Mariae Zone).

Description. - The adult stage of O. pidanceti is unknown yet. It is supposed to exhibit an angle in the bodychamber. The sculpture of the phragmocone strongly resembles the oppellid genus Tarameliceras. On the siphonal side at both sides of the prominent fienly serrate keel smooth areas occur, which may be sometimes slightly depressed. The inner whors do not exhibit any keel; they possess a smooth venter. In contrast to taramelliceratids, we recognize an unusually broad cross section and the lack of any ventromarginal nodes. In some well preserved specimens a spiral ornamentation occurs on the flanks of the conch. Following the literature, the ammonite species Oxydiscites
pidanceti (COUAND) has only been found once by the holotype. We assume, however, that inner whorls of this species may have been overlooked or they were not recognized because of their resemblance to oppellids, especially taramellerceratids. For example, such specimens were included by LORIOL (1900, pl. 3, figs. 21-23, non figs. 17-20) in Oppelia episcopalis. They differ from the latter by their broader cross section (“var. globosa”), a stronger involution and especially in the development of a keel from a dense row of punctuated nodes. LORIOL (1900: 42) himself remarked a possible relationship of these “unique monstrosities” to the co-occurring Ammonites calcaratus COUAND. However, he felt their suture lines being too different to include his specimens into the latter species. The reason for this difference is that the suture line becomes more complicated in the adult stage. In the microconchs the suture line remains at a primitive stage. In a very well preserved specimen, LORIOL even noticed a spiral stigitation on the shell, which must be taken as a further hint, that these are inner whorls of a species belonging to Oxydiscites. Identical observations can be made in the specimens described from the Lower Oxfordian of Mount Hermon, Syria (HAAS 1955). From there, the inner whorls of a macroconch are figured besides a microconch specimen (see below).

The finding level of most specimens can be located precisely in the Praecordatum Subzone of the Lower Oxfordian. A recently found juvenile specimen from the French Calvados coast (Fig. 6), however, comes from the “Marnes de Villers” Formation which is Mariae Zone in age according to the Cardioceras fauna (pers. comm. A. Ilo, Düsseldorf, lithological unit H13 of HERR 1860). This specimen differs from typical O. pidanceti by its well developed ribbing stage with ventral nodes and a broader cross section. Although pyritized, it shows a weak but remarkable spiral stigitation. Another specimen described by ARKELL (1939) from the Woodham section also comes from the Mariae Zone.

Measurements:

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Oxydiscites geyeri n. sp.

Fig. 8


- [Nomen nudum]

v 1971 Ochetoceras (Oxydiscites?) n. sp. – WENDT, p. 162.

Holotype: Specimen figured on Fig. 8, housed at the GPIT, no. 1855.

Locus typicus: Rocca Busambra, W Sicily, Italy.

Stratum typicum: Neptunian dyke which yields the ammonite fauna 14 in the section 1 in WENDT 1971; age after co-occurring taxa: Transversarium Zone.

Derivation nominis: In honour of the 75th birthday of our teacher, friend and colleague Prof. Dr. O. F. GEYER, who was the first to describe specimens of Oxydiscites laffoni besides the holotype.

Occurrence: Sicily, SW Germany or E Switzerland.

Material: Holotype only.

Diagnosis: Relatively large species of Oxydiscites without undulating keel, showing a lateral groove on the bodychamber.

Description. – The holotype is an uncompressed steinkern with some remains of the shell. The matrix is a mudstone of a light pink to reddish colour. The specimen appears to be almost adult. Small parts of the peristome were obviously broken away before the embedding. At the beginning of the last whorl the shell is excellently preserved and exhibits a spiral ornamentation and a conspicuous angle in the bodychamber. On the inner whorls the cross section is oval with a very thin and finely serratke keel. Later the conch becomes oxyzony, whereas in the last sculptural stage the venter is almost rounded. The wall of the umbilicus is rather steep. The sculpture consists of falcoid ribs. The radiate primaries are gradually expiring towards the bodychamber. On the last whorl a shallow lateral groove sets in somewhat below the middle of the flank. This groove shifts to a higher position on the bodychamber. It ends just behind the peristome. On the outer flank the ribs are falcoïd, later they become strongly rectiradiate. Several changes in the orientation of the sculpture are present. Just before the end of the bodychamber the ribs curve forward and tend to bifurcate. This last change in the direction of the ribbing may be the result of a shell injury.

Comparisons. – O. geyeri n. sp. differs from O. margaritatus (CARIOU & SEQUEIROS) and O. pidanceti (COUAND) by a sculptural stage showing a shallow lateral spiral groove. The other morphological features are almost identical. O. multiformis (GROSSGOL figures) exhibits a wider umbilicus. O. laffoni (MOESCH), and the other chronospecies from youn-
ger stratigraphical levels possess a lateral undulation of the keel and a narrower umbilicus.

Remarks. – After WENDT (1971) the holotype specimen of O. geyeri n. sp. comes from his faunal association 16. From this association, he listed almost exclusively ammonite taxa indicating a Lower Kimmeridgian age. After the original label and the lithofacies, however, the specimen belongs to his faunal association 14, so that the published statement seems to be erroneous. The ammonite species listed from fauna 14 and especially from the same site were checked in the Tübingen collection. They clearly indicate a Middle Oxfordian age (Transversarium Zone). Surprisingly, a comparison of the fauna resulted in a almost complete identity of this fauna with an ammonite fauna known from the Mumienkalk in the Wutach area of SW Germany and the adjacent Birmenstorf beds in Switzerland. It is very likely that the specimen which ROLLER (1909) intended to describe as "Oxydiscites Merkleini n. sp." came from this level. ROLLER indicated the finding level as "Argovien inférieur" of the Randen area, which is synonymous with the Birmenstorf beds and the Mumienkalk.

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Oxydiscites laffoni (MOESCH) Fig. 11-14

v 1867 Ammonites laffoni. – MOESCH, p. 293, pl. 1, fig. 4.

v 1964 Ochetoceras (Oxydiscites) laffoni (MOESCH). – HÖROLDT, p. 93, pl. 6, fig. 8.


Holotype: Specimen figured by MOESCH 1867, pl. 1, fig. 4, housed in the collection of the ETH Zürich, Switzerland.

Locus typicus: Randen area (Switzerland, Kanton Schaffhausen).

Stratum typicum: Lowermost Schwarzbach Formation, Lower Kimmeridgian, Platynota Zone, Polygyratus Subzone sensu AMROPS.

Occurrence: S Germany (Swabia and Franconia), NE Switzerland (Canton Schaffhausen), SE France, S Spain.

Description. – See the full description in SCHWEIGERT (1995), which was based on several differently preserved specimens, some of them even uncompressed. In one specimen of those, a spiral ornamentation was remarked but not valued taxonomically. In other well preserved specimens sometimes a spiral ornamentation is visible at the beginning of the bodychamber, as it can be seen in a recently discovered specimen (Fig. 11) from the Platynota Zone of Geisingen/Donau (W Swabia).

For measurements see SCHWEIGERT (1995).

Oxydiscites ellipticus (OLÓRIZ) Fig. 17

1978 Metastreblites ellipticus n. sp. – OLÓRIZ, p. 55, pl. 2, figs. 1-2.

1995 Oxydiscites ellipticus (OLÓRIZ). – SCHWEIGERT, p. 4. – [With further synonyms]

Holotype: Specimen figured by OLÓRIZ 1978, pl. 2, fig. 1, refigured herein.

Locus typicus: Sierra Gorda, S Spain.

Stratum typicum: Lower Kim-meridgian, Hypselocyclum Zone (? – lowermost Divisum Zone).

Occurrence: Subbetic Jurassic of S Spain, Morocco (Prerif).

Oxydiscites ellipticus differs from O. laffoni by its very pronounced angle of the bodychamber and by a higher position of the lateral nodes on the flanks. The few specimens known belonging to this species are larger than all specimens of O. laffoni under study. However, most of the latter are not fully grown or imperfectly preserved.

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Oxydiscites praesemiformis (OLÓRIZ)

1978 Metastreblites praesemiformis n. sp. – OLÓRIZ, p. 56, pl. 2, fig. 3, pl. 3, fig. 11.

1995 Oxydiscites praesemiformis (OLÓRIZ). – SCHWEIGERT, p. 4. – [With synonyms]

Holotype: Specimen figured by OLÓRIZ 1978, pl. 2, fig. 3, pl. 3, fig. 11.

Locus typicus: Sierra Gorda, S Spain.

Stratum typicum: Lower Kimmerid-gian, Hypselocyclum Zone.

Occurrence: Subbetic Jurassic of S Spain, S Alps (N Italy).
Fig. 12. *Oxydiscites laffoni* (Moeschi). Lower Kimmeridgian, Platynota Zone, Lacunosamergel Formation, Böttingen/Heuberg, W Swabian Alb. SMNS no. 62606 (leg. G. Hak). – x1.

Fig. 13. *Oxydiscites laffoni* (Moeschi). Lower Kimmeridgian, Platynota Zone, Lacunosamergel Formation, Hausen im Tal, W Swabian Alb. SMNS no. 62611 (leg. B. Russ). – a: Ventral view, b: Lateral view – x1; c: enlarged part showing the spiral strigation.

Fig. 14. *Oxydiscites laffoni* (Moeschi), with remarkable spiral ornamentation. Lower Kimmeridgian, Platynota Zone, Lacunosamergel Formation, Geisingen, W Swabian Alb. SMNS no. 63463 (leg. G. Herold, ex Coll. V. Schlamp). – x1.

Fig. 15. *Sphaerodomites ebeli* (Schweigert), holotype. Lower Kimmeridgian, Platynota Zone, Lacunosamergel Formation, Hausen im Tal, W Swabian Alb. SMNS no. 26832 (leg. K. Ebel). a, b: Lateral views, c: Ventral view. – x1.5.

Fig. 16. *Sphaerodomites ebeli* (Schweigert), specimen from fig. 10. Lower Kimmeridgian, Platynota Zone, Neptunian dyke "Ambrosi" near Breonio, W Monti Lessini, Province of Verona. MFL, no. G.A.I. 52 (leg. A. Benetti). a, b: Lateral views, c, d: Ventral views. – x1.5.

Fig. 17. *Oxydiscites ellypticus* (Olóriz), holotype. Lower Kimmeridgian, Strombecki Zone, Sierra Gorda, S Spain. Universidad de Granada collection, no. F.G15.7.13. a: Lateral view, b: Ventral view. – x1.
Regarding the variability in other species of *Oxydiscites* the taxonomic separation of *O. praesemiformis* from *O. ellipticus* remains somewhat doubtful. A smooth depression on the ventral part of the bodychamber, which was said to be characteristic of *O. praesemiformis* and not present in *O. ellipticus*, is already anticipated in large specimens of the much older chronospecies *O. margaritatus*. At the moment it is not possible to decide whether really two separate taxa are present at the same time, or both are linked by transitions, because of the very small number of specimens available.

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### 3.2 The microconchs: *Sphaerodomites*

**Genus Sphaerodomites** **ROLLIER 1909** [m]

(Synonym: Barthelia Olóriz & Schairer 1983)

**Emended diagnosis:** Sphaerocone shell with scaphitoid last whorl, minute umbilicus, finely serrate keel accompanied by smooth bands or shallow grooves, falcoid to polyschizotome ribbing, aperture with lappets and a hook-like umbilical thickening, spiral striation present in well preserved specimens.

**Type species:** *Ammonites calcaratus* **COQUAND 1853.**

*Sphaerodomites calcaratus* (COQUAND)  
*Fig. 4*

*1853* *Ammonites calcaratus.* – **COQUAND, p. 441**, pl. 14, fig. 7-8.

1866 *Ammonites calcaratus* **COQUAND.** – **OPPEL, p. 217.**

1898 *Oppelia ? calcarata* (COQUAND). – **LORIOL, p. 61**, pl. 5, fig. 2.

1900 *Oppelia ? calcarata* (COQUAND). – **LORIOL, p. 51**, pl. 4, fig. 9.

1909 *Sphaerodomites calcaratus.* – **ROLLIER, p. 9.**

1928 *Oppelia (Phlycticeras?) calcarata* **COQUAND.** – **MAIRE, p. 52**, pl. 3, fig. 16-17.


1983 *Sphaerodomites calcaratus* **COQUAND.** – **OLÓRIZ & SCHAIRER, fig. 4.1-4.2.**

**Holotype:** Specimen figured by **COQUAND 1853, pl. 14, fig. 7-8** (probably lost).

**Locus typicus:** "Palente", city area of Besançon.

**Stratum typicum:** Marnes à Renggeri, Lower Oxfordian, Cordatum Zone, Praecordatum Subzone.

**Occurrence:** Franche-Comté, E Switzerland.

The holotype of *Sphaerodomites calcaratus* exhibits a unique sculptural element which inspired **COQUAND** to this specific name. The normal ribbing is interrupted by a single rib which crosses the ventral part of the phragmocone in the shape of a ring. All specimens which were found later did not exhibit this strange ribbing so that it represents surely nothing but a rare pathology of the "forma circumdata" type of **HÖLDER** (1956). The holotype specimen was refigured by **LORIOL** (1900, pl. 4, fig. 9).

The remarkable tentative classification of *Ammonites calcaratus* **COQUAND** into the genus *Phlycticeras* of **MAIRE** (1928) was caused by the strange comparison with an ammonite erroneously determined by **BUCKMAN** (1914: 99) as *Phlycticeras*, which is in fact, however, a *Chamosussetia* (see **CALLOMON & WRIGHT 1989**).

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**Sphaerodomites reynelensis** (**MAIRE**)

? 1909 *Sphaerodomites margarita* n. sp. – **ROLLIER, p. 9.** – [Nomen nudum]

*1928* *Oppelia (Phlycticeras?) reynelensis.* – **MAIRE, p. 51**, pl. 3, fig. 16-17, 24.

**Lectotype:** Specimen figured by **MAIRE 1928**, pl. 3, fig. 18-19 (University of Lyon, MAIRE collection), designated herein.

**Locus typicus:** Reynel, Dept. Haute-Marne, France.

**Stratum typicum:** Marnes à Renggeri, Lower Oxfordian, Cordatum Zone, somewhat younger level than that of *S. calcaratus*.

**Occurrence:** Eastern and South-Eastern France (Franche-Compté).

**Description.** – Compared with *S. calcaratus*, this species is remarkably smaller and exhibits a slender cross section. Moreover, the ribs are more gracile. The ventral grooves on both sides of the keel are only developed over a very short di-
stance just before the beginning of the bodychamber. In some well preserved specimens a strigation is visible on the test (Coll. B. HOSTETTLER, Gloveller/CH). Obviously this strigation was already noticed by MAIRE (1928: 52) who reported the occurrence of "filets spiraux latéraux", although his figured specimens do not show a strigation.

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Holotype: Specimen figured by OLÓRIZ & SCHAIRER, 1983, fig. 1/1-4, refugured herein.

**Sphaerodomites subbeticus** (OLÓRIZ & SCHAIRER)

Fig. 9

v*1983 Barthelia subbetrica. – OLÓRIZ & SCHAIRER, p. 578, fig. 1/1-4, 2.

v 1988 Barthelia sp. – BENETTI & PEZZONI, fig. 1.

1995 Barthelia subbetrica OLÓRIZ & SCHAIRER. – SCHAIRER, p. 5, pl. 1, fig. 9.

Holotype: Specimen figured by OLÓRIZ & SCHAIRER 1983, fig. 1/1-4, refugured herein.

**Locus typicus:** Sierra Quipar, Prov. Murcia, S Spain.

**Stratum typicum:** Upper Oxfordian, Bimammatum Zone (cf.-specimen from the Planula Zone).

**Occurrence:** Subbetic and Prebetic Upper Jurassic of Southern Spain, Southern Alps (Monti Lessini, Prov. Verona). Most probably the lost holotype of *"Oecoptychius albus FISCHER"* from the Swabian Upper Jurassic also belongs to this species.

**Description.** – See OLÓRIZ & SCHAIRER 1983; OLÓRIZ et al. 1991. A morphological feature of this species, which has been formerly overlooked, but which is even visible in the rather poorly preserved holotype, is the finely crenate keel. Exactly the same type of keel is developed in *Sphaerodinutes ebelii*.

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Holotype: Specimen figured by OLÓRIZ & SCHAIRER, 1983, fig. 1/1-4, refugured herein.

**Sphaerodinutes ebelii** (SCHAIRER)

Fig. 10, 15-16

v*1995 Barthelia ebeli n. sp. – SCHAIRER, p. 5, pl. 1, fig. 8 a-f.

Holotype: Specimen figured by SCHAIRER, 1995, pl. 1, fig. 8, SMNS no. 26832.
ted for the first time from the Southern Alps, also "Lingulaticeras filaur" (Oppel)" and the inner whorls of a perisphinctid determined as "Nebroditès macerimus" may come from the Platynota Zone. The latter resembles "Perisphinctes" pseudobifurcatus Cheffiat. This species occurs in the basal Platynota Zone of Swabia and Franconia (Scharer & Schlamp 1995), there termed as "Idoceras (Subnbrodites sp.)." All these data support the assumption, that the new specimen of Sphaerodomites ebeli comes from the Platynota Zone, as the holotype does.

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4 OTHER TAXA NOT RELATED TO OXYDISCITES

It was pointed out by Schweigert (1995) that the boreal or subboreal oppelids from the Far East of Russia and from Greenland, by several authors tentatively assigned to Oxydiscites, are much closer related to Ochetoceras. For these ochetoceratids which may have migrated into the subboreal realm, the new genus Suboxydiscites was introduced by Poulton et al. (1988).

5 ON THE PHYLOGENETIC HISTORY OF OXYDISCITES AND THE PHYLCICERATINAE

As shown above, the discovery of a dimorphism between Oxydiscites and Sphaerodomites allows to trace back now the history of the genusGattung Oxydiscites into the Late Callovian (Athleta Zone). Again the question for the phylogenetic roots of this genus arises. At this point an unusual morphological feature must be noticed, which is only exceptionally visible in well preserved specimens: a strigoceratid spiral ornamentation on the test. Such a spiral ornamentation is present in Oxydiscites laffoni (Moesch) at the beginning of the last whorl, where it was overgrown by the test of the body chamber. A very weak strigation is also visible on the steinkern of Sphaerodomites ebeli from Northern Italy described above. A spiral strigation is characteristic of the Jurassic ammonite family Strigoceratidae, but it is unknown from true oppelids. It was Rollier (1909) who already compared Oxydiscites with Ammonites dorsocavatus Quenstedt, which he assigned to Strigoceras, just as Quenstedt (1886-87) did. This ammonite was recently recognized as belonging to Phlycticeras. The stratigraphically youngest member of the Strigoceratidae was thought to be the genus Phlycticeras, which reached the base of the Late Callovian (Athleta Zone, Trezeense Subzone) with the chrospecies P. waageni Buckman (Schweigert & Dietze 1998). Phlycticeras exhibits exactly the same type of keel as Oxydiscites, which is characterized as a rather high, razor-sharp, serrate, and sometimes even undulating, easily dropping off septircinate keel. Until recently, the antidimorphs which correspond to Phlycticeras could not be identified. Callomon (in Donovan et al. 1981) remarked that possibly the genus Oecoptychius could be the wanted antidimorphs, but strong arguments against this view have been put forward (see Dietl 1986). One of the strongest arguments against this dimorphism was the postulated absence of a spiral strigation in Oecoptychius. In fact, most of the calcareous or pyritized casts show a smooth surface, but sometimes specimens with a partly preserved shell were detected. In these exceptionally well preserved specimens a spiral strigation could be observed (Schweigert & Dietze 1998, pl. 6, fig. 5; pl. 9, fig. 8-9). Another strong argument against this proposed dimorphism was the lacking of a keel in Oecoptychius. In a very juvenile growth stage, however, Phlycticeras also lacks a keel, whereas it is to suppose that Oecoptychius gets adult until a keeled stage is developed. The ribbing of the inner whors is strikingly similar in both genera. The occurrence of an extremely thickened shell around the umbilicus, which was remarked by Dietl (1986) in a specimen of Oecoptychius subrefractus (Buckman) with preserved shell, is similarly present in the new specimen of Sphaerodomites ebeli (Schweigert). The sutureal development is absolutely identical in the early growth stages of Oecoptychius and Phlycticeras. Schweigert & Dietze (1998, 1999) searched for the missing Phlycticeras of the Late Bajocian and of the Early Bathonian, because in strata of these ages Oecoptychius is already present, although extremely rare. In fact, early phlycticeratins were described both from the Late Bajocian and from the Early Bathonian, but they had not been recognized as Phlycticeras but were taken as Strigoceras or included in other genera. A revision of the genus Phlycticeras in which all arguments towards a dimorphism with Oecoptychius are discussed, was recently published by Schweigert & Dietze (1998).

Now, we can regard the dimorphism between the ammonite genera Phlycticeras [M]/Oecoptychius [m] rather well established, and we interpret both phlycticeratids and Oxydiscites [M]/Sphaerodomites [m] as descendants from the same stock within the Strigoceratidae. A close ancestor of
Oxydiscites may be represented by the Bathonian genus Strungia Arkell.

The Upper Jurassic ammonite genus Cymaceras cannot be related directly to Oxydiscites because of its differing microconch counterpart Trochiskioceras, but also Cymaceras may have its roots within the Strigoceratidae (Phlycticeratinae). It was Wegele (1930) who noticed a striking similarity in the sculptural development between Cymaceras and Phlycticeras. However, he immediately discarded this idea, because of the enormous stratigraphical gap between both occurrences and the lacking of a spiral striation in Cymaceras. Soon later, however, Kühn (1933) published a well preserved specimen of Cymaceras in which such a striation is clearly visible. Schärer & Schlamp (1991, pl. 1, fig. 22) figured another specimen of Cymaceras guembeli Oppel again showing a spiral striation, but these authors have not drawn any conclusions concerning the systematic position of this genus. In Ochetoceras, a spiral striation is virtually absent, which is why this genus might not have a very close relation to Cymaceras. The anti-dimorph of Ochetoceras – Glochiceras s. str. – differs strongly from the enigmatic microconch genus Trochiskioceras Schärer & Schlamp, but both exhibit a constriction and a small horn just behind the perisome with the lappets.

Obviously nearly forgotten was the interesting view of Rollier (1909), who included Ammonites guembeli Oppel in his proposed genus Porticlercia, which was established in 1911 according to the nomenclatorial rules (type species: Ammonites mirobibilis De GROSSouRRE). The dimorphic partner of Porticlercia is hitherto unknown. After the polychizotome style of ribbing we consider that the latter genus also originates in the Phlycticeratinae lineage (see Schweigert & Dietze 1998). Most probably Porticlercia split off not before the Early Callovian because of its three rows of tubercles, which are also present in Phlycticeras mexicanum Sandoval & Westermann.

As a result light was shed on the mystery of the phylogenetic relations of some "classical" examples of ammonite genera like Oecoptychus or Phlycticeras which were said to occur rather suddenly in earth history (Neumayr 1878) in view of their dimorphism. The phlycticeratines are surely no direct descendants of Strigoceras, but a parallel lineage (Phlycticeratinae). The dimorphic genera Oxydiscites/Sphaerodromites clearly represent another rather early offshoot of this lineage.

The Tithonian scaphitoid ammonite genus Semiformiceras is superficially similar to Oxydiscites, but regarding its microconch antidiomorph Cyrtosiceras a derivation from the Streblitinae is much more likely than from the Phlycticeratinae.

6 ACKNOWLEDGEMENTS

Gerd Dietl (SMNS) and John Callomon (University College, London) are thanked for numerous fruitful discussions on ammonite dimorphism. Elie Cariou (University of Poitiers, France), Bernhard Hostettler (Glovelier/CH), August Ilg (Düsseldorf), Alexander Liebau (GPIT), Féderico Olóriz (Granada, Spain), Burkhardt Russ (Nusplingen, Germany), Gerhard Schalier (Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich), Viktor Schlamp (Friedberg) and Annick Bouillier-Rollet (University of Franche-Comté, Besançon) kindly provided specimens or plaster casts for this investigation. Jost Wendt (GPIT) kindly allowed to include material from his collections from Sicily housed at the GPIT.

7 REFERENCES


– (1911): Les Fazies du Dogger ou Oolithique dans le Jura et les Régions voisines. 352 pp., 59 figs., 9 tables; Zürich (Georg).


