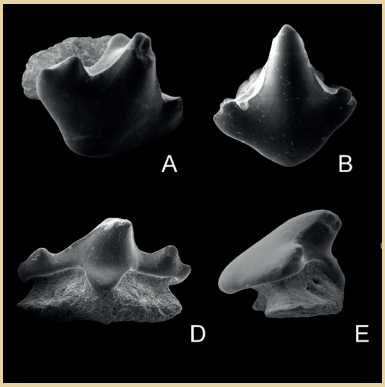
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Palaeobiology of the early Toarcian of Luxembourg

Robert Weis
Ben Thuy
(editors)

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2. *Dactylioceras* (*Microdactylites*) *attenuatum* (Simpson, 1855), TI008b.
3. *Thiesoscyllium underwoodi* nov. gen., n. sp. (A, D - TM579, paratype 1, labial and lingual view; B - TM580, Holotype, labial view; E. TM582, paratype 3, profile view).

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The ammonite fauna of the Bifrons Zone (Lower Toarcian) of Sanem and Soleuvre (Grand-duchy of Luxembourg)

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Keywords: Ammonites, taxonomy, Hildoceratidae, Dactylioceratidae, Lytoceratidae, Phylloceratidae, 'Couches à Hildoceras bifrons', lower Toarcian.

Abstract

An important collection of fossils recovered from limestone nodules, commonly referred to as 'Bifronsknollen', has been examined. These nodules date from the lower Bifrons Zone of the Toarcian stage; they originate from temporary outcrops exposed during earthworks for the construction of the motorway A13 during the 1990s, in the vicinity of the villages of Sanem and Soleuvre. From these nodules, more than 430 well-preserved ammonite specimens were investigated, allowing the recognition of eight genera, four subgenera, and thirteen species: *Phylloceras heterophyllum*, *Lytoceras* (*Trachylytoceras*) *nitidus*, *Alocolytoceras dorcadis*, *Dactylioceras* (*Dactylioceras*) *holandrei*, *D.* (*D.*) *athleticum*, *D.* (*D.*) *commune*, *D.* (*D.*) *crassiusculum*, *D.* (*Microdactylites*) *attenuatum*, *Nodicoeloceras dayi*, *Nodicoeloceras* sp. ind., *Harpoceras* (*Maconiceras*) *soloniacense*, *Hildoceras lusitanicum*, and *Frechiella subcarinata*. This assemblage is typical for the Sublevisoni Subchronozone in Western Europe.

Schlüsselwörter: Ammoniten, Taxonomie, Hildoceratidae, Dactylioceratidae, Lytoceratidae, Phylloceratidae, 'Schichten mit Hildoceras bifrons', Unter-Toarcium.

Zusammenfassung

Eine bedeutende Sammlung von Fossilien, gefunden in Kalkstein-Knollen, die gemeinhin als "Bifronsknollen" bezeichnet werden, wurde untersucht. Diese Knollen stammen aus der unteren Bifrons-Zone des Toarciums und wurden in den 1990er Jahren bei Erdarbeiten für den Bau der Autobahn A13 in der Nähe der Dörfer Sanem und Soleuvre freigelegt. Aus diesen Knollen wurden mehr als 430 gut erhaltene Ammoniten-Exemplare untersucht, wodurch acht Gattungen, vier Untergattungen und dreizehn Arten identifiziert werden konnten: *Phylloceras heterophyllum*, *Lytoceras* (*Trachylytoceras*) *nitidus*, *Alocolytoceras dorcadis*, *Dactylioceras* (*Dactylioceras*) *holandrei*, *D.* (*D.*) *athleticum*, *D.* (*D.*) *commune*, *D.* (*D.*) *crassiusculum*, *D.* (*Microdactylites*) *attenuatum*, *Nodicoeloceras dayi*, *Nodicoeloceras* sp. ind., *Harpoceras* (*Maconiceras*) *soloniacense*, *Hildoceras lusitanicum* und *Frechiella subcarinata*. Diese Vergesellschaftung ist typisch für die Sublevisoni Unter-Chronozone in West-Europa.

Mots clés: Ammonites, taxonomie, Hildoceratidae, Dactylioceratidae, Lytoceratidae, Phylloceratidae, 'Couches à Hildoceras bifrons', Toarcien inférieur.

Résumé

Une importante collection de fossiles récupérés dans des nodules calcaires, communément appelés " Bifronsknollen ", a été examinée. Ces nodules datent de la partie inférieure de la zone à Bifrons, au Toarcien ; ils proviennent d'affleurements temporaires mis à jour lors des travaux de terrassement pour la construction de l'autoroute A13 dans les années 1990, à proximité des villages de Sanem et Soleuvre. À partir de ces nodules, plus de 430 spécimens d'ammonites bien conservés ont été étudiés, permettant la reconnaissance de huit genres, quatre sous-genres et treize espèces : *Phylloceras heterophyllum*, *Lytoceras* (*Trachylytoceras*) *nitidus*, *Alocolytoceras dorcadis*, *Dactylioceras* (*Dactylioceras*) *holandrei*, *D.* (*D.*) *athleticum*, *D.* (*D.*) *commune*, *D.* (*D.*) *crassiusculum*, *D.* (*Microdactylites*) *attenuatum*, *Nodicoeloceras dayi*, *Nodicoeloceras* sp. ind., *Harpoceras* (*Maconiceras*) *soloniacense*, *Hildoceras lusitanicum* et *Frechiella subcarinata*. Cet assemblage est typique de la sous-chronozone à Sublevisoni en Europe occidentale.

1 Introduction

An abundant ammonite fauna, accompanied by numerous other invertebrate fossils, is preserved in the palaeontological collections at the National Museum of Natural History in Luxembourg. The specimens, collected during excavations for the A13 motorway in southern Luxembourg during the 1990s close to Sanem and Soleuvre, are well preserved and originate from nodules known as 'Bifronsknollen' (Lucius 1945) - literally "Bifrons nodules" - which occur in the 'Couches à *Hildoceras bifrons* (lo2)' member as reported on the geological map of southern Luxembourg (Lucius 1945). Past temporary outcrops had shown that the nodules occur in several, probably up to four, separate beds (R. Weis, personal communication 2025); however, no formal fieldwork campaign has been undertaken to confirm this, and all fossils herein studied originate from private collections, without finer stratigraphic information.

Only a few previous studies have addressed this material, from the perspective of ammonite taphocoenosis (Maubeuge 1970), and brachiopod assemblages (Di Cencio & Weis 2023). It is the latter study that initiated a tentative correlation with analogous coeval trans-European associations.

The present work aims to provide a systematic study of the ammonite assemblage that will serve as basic information for further studies investigating in more detail the taphonomy and biostratigraphy of these beds.

2 Geological setting and material

The fossil assemblages described herein are found within carbonate nodules distributed in up to four separate levels, embedded in grey-brown marlstone that outcrops in the area around Sanem and Soleuvre, in southern Luxembourg (Fig. 1). In the present study, the levels containing the nodules under investigation belong to the lithotype known in Luxembourg as the *Couches à Hildoceras bifrons* (lo2*)* (Lucius, 1945). The same lithotype is referred to in Belgium as the *Marnes de Grandcourt* (Boulvain et al. 1995) and in Lorraine (France) as the *Marnes à Bifrons* (Hermoso 2007). The nodules contain a characteristic invertebrate association that has been partially studied by Maubeuge (1970) and Di Cencio & Weis (2023). The top of some nodules shows an accumulation of belemnite rostra forming 'belemnite battlefields' (Doyle & Macdonald 1993). These limestone nodules, which have been referred to as 'Bifronsknollen' by Lucius (1945), contain extremely abundant, well-preserved invertebrate fossils (ammonites, nautilids, belemnites, brachiopods, bivalves, microgastropods) along with rare, disarticulated vertebrate and vegetal remains. The concentration and preservation of these fossils render them suitable already for designation as a *Konzentrat-Lagerstätte* sensu Seilacher (1970). Di Cencio & Weis (2023) provided the first detailed investigation of the palaeontological associations within the 'Bifronsknollen' nodules, with particular emphasis on the presence of the 'disaster marker' (Emig 1997; Di Cencio et al. 2021) *Lingularia longoviciensis*. In addition to *Lingularia longoviciensis*, the faunal assemblage includes the brachiopod *Discinisca papyracea*, thin-shelled bivalves such as *Meleagrinella substriata* and *Bositra buchii*, belemnites referable to *Acrocoelites* spp., and isolated selachian remains (including spines and teeth) attributed to *Hybodus* (Delsate 1997). Small, presumably planktonic gastropods belonging to the genera *Globorilusopsis* and *Simoniceras* are also present, although they were previously misidentified as Calyptoptomatida by Maubeuge (1998). From a biostratigraphic perspective, the presence of characteristic ammonites indicates the lower part of the Bifrons Chronozone and more specifically the Sublevisoni Subzone (see Elmi et al. 1997 for a comprehensive zonation of the NW European Toarcian).

3 Material & Methods

Over 430 identifiable ammonite specimens have been examined, displaying various states of exposure - ranging from fully exposed fossils free from matrix to those embedded within the sediment. Specimens that were severely affected by taphonomic processes and thus unable to yield significant accessory information were excluded from the study. Of course, poorly preserved specimens were nonetheless included when they represented taxonomic novelties, unique examples, or displayed diagnostic features of classificatory importance.

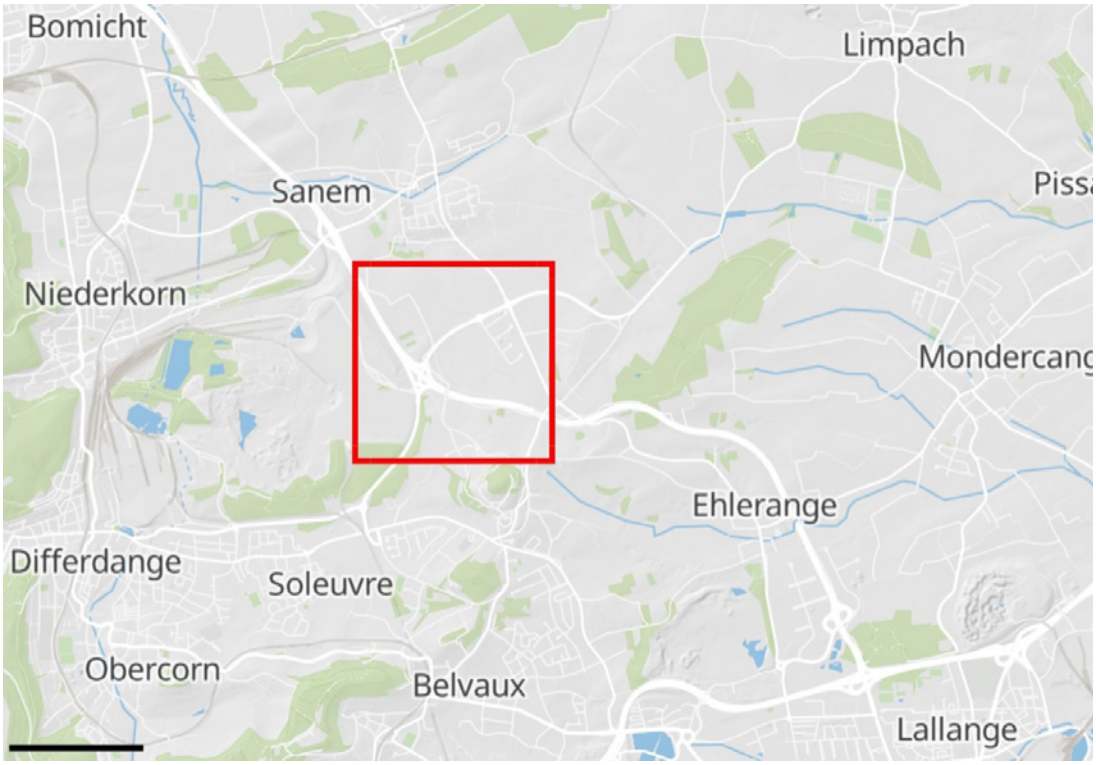


Fig. 1: The geographic view of the area between Sanem and Soleuvre in southwestern Luxembourg (modified by https://map.geoportail.lu/). In the red square, the area where most of slabs with ammonites were sampled. Scale bar: 1 km long.

All specimens initially originate from private collections, whose holders were also responsible for their preparation; recently, all the material has been acquired as part of the public collection of the National Museum of Natural History in Luxembourg (acronym: MNHNL). Each sample - whether a fossil slab or an individual specimen - is catalogued with a code consisting of a pair or triplet of capital letters (e.g. TM), followed by a three-digit number (e.g. 418). When a slab (e.g. TM418) contains multiple specimens, each is further designated by a lowercase letter (e.g. TM418a). All slabs were photographed, and explanatory photographic files complete with legends were produced.

Photographic documentation was obtained using a Motorola G35 5G smartphone equipped with a 50MP camera. The figures and plates included in this study were generated by editing the photographic files using the online platform www.canva.com.

Regarding the descriptions of ammonites and their supraspecific classification, the starting point adopted in the present study is the *Treatise on Invertebrate Palaeontology* (Arkell et al. 1957; Howarth 2013; Hoffmann 2015). Concerning elements of the suture lines, reference is made to Venturi and Ferri (2001) and Di Cencio (2007).

4 Systematic Palaeontology

Class Cephalopoda Cuvier, 1797
Subclass Ammonoidea Zittel, 1884
Order Phylloceratida Arkell, 1950
Suborder Phylloceratina Arkell, 1950
Superfamily Phylloceratoidea Zittel, 1884
Family Phylloceratidae Zittel 1884
Subfamily Phylloceratinae Zittel 1884

Genus *Phylloceras* Suess, 1865

Phylloceras heterophyllum (Sowerby, 1820)
(Pls. 1, 2)

* 1820 *Ammonites heterophyllus* Sowerby, p. 119, pl. 266.

1841 *Ammonites Terverii* d'Orbigny, p. 179; pl. 54.

1975 *Phylloceras heterophyllum* (Sowerby, 1820) forme *plicatum* Joly, p. 1086, pl. 1, fig. 2a, b, Fig. 2.

2000 *Phylloceras heterophyllum* (Sowerby); Joly, p. 43, figs. 72-78; pl. 5, figs. 1, 2; pl. 6, figs. 1, 2a, b, 3.

2000 *Phylloceras heterophyllum* (Sowerby, 1820) *plicatum* Joly 1975, Joly, p.; pl. 4, figs. 12, 13.

2007 *Phylloceras heterophyllum* (Sowerby) *plicatum* Joly; Rulleau, p. 45; p. 51, fig. 10/1; pl. 1, fig. 2a.b.

v. 2007 *Phylloceras heterophyllum* (Sowerby, 1820), Di Cencio, Tav. I, Figs. 1, 4, 5, 7, 9-15; Tav. II, 1, 2, 4-8; Tav. IV, 9, 10, 12.

Holotype - The species is established on *Ammonites heterophyllus* by Sowerby (1820: 119, pl. 266).

Material - Fifteen specimens **(**MNHNL TI009, TM429, 473, 461, 509f, TU141d, 143, 405b, 407b, 979, TV446, 518, 524b, 565a, 877c).

Description - Involute planispiral shell with rapidly expanding whorls that completely conceal the inner coils. The whorl section is sub-oval and relatively compressed, being higher than wide. The greatest width is located ventrally, with gently rounded flanks converging towards both the venter and the umbilical area. The venter is broad and rounded; the umbilicus is entirely closed. Ornamentation is usually absent, except for preserved growth lines on the pseudo-shell, which are sinuous and prosocline. In some specimens, these may appear bundled and may exhibit weak internal mould constrictions. This ornamentation style may, in some cases, remain impressed on the internal mould. In the gigantic specimen TI009, nicknamed *Cornucopia* [a name of Latin origin that literally means "horn of abundance", owing to the peculiar accumulation of *Dactylioceras* fossils near the aperture, as if they had been produced by the *Phylloceras* itself (pl. 3)] with a shell diameter of 35 cm, morphological changes become apparent. The coiling becomes less involute, exposing the umbilicus, with an evolute index of approximately 0.13. The flanks appear relatively lower in height compared to the shell's thickness, yielding a compression index of around 0.61. On the final whorl, flank undulations become apparent and develop into rounded ribs. These ribs arise subtly at the umbilical margin, become more pronounced around the inner third of the flank, and fade slightly beyond mid-flank. Their trajectory mirrors that of the growth lines—initially prosocline, followed by a gentle backward curvature—giving a slightly sinuous appearance. The peristome is preserved and appears as a simple, prosocline, sinuous aperture resembling the described ribbing pattern. The suture line is of the pentalobate phylloceratine type, with relatively intricate and frilled elements. The external lobe (E) is broad and shallow, with an accessory saddle (A); the external saddle (ES) is narrow and bifid; the lateral lobe (L) is deeper than E and finely lacinated. The first lateral saddle (LS_1) is finely ornamented, with a narrow, frilled body and trifid termination. Umbilical elements follow a pattern similar to that of the lateral elements.

Remarks - *Phylloceras heterophyllum* is distinguished from other species primarily in terms of general shell morphology and certain features of the suture line. The diagnostic characteristics of the external and lateral saddles—bifoliate and trifoliate, respectively (Joly 2000)—allow for a confident attribution to the species *heterophyllum* and a clear distinction from all coeval phylloceratins. The ornamentation of the pseudo-shell, consisting of fasciculate striae, remains impressed on the internal mould of the fossil. Due to a similar feature, Joly (1975) established the subspecies *P. h. plicatum*. This name has been employed in the literature over time (Rulleau 1998, 2007; Joly 2000); however, in the present study, this subspecies is considered synonymous with the nominal species. It is proposed that the ornamentation observed on the internal moulds of these ammonites merely reflects the imprint of the external shell upon the internal cast.

Occurrence - *Phylloceras heterophyllum* is present throughout the Toarcian, with a more consistent distri-

Plate 1: **a, b** - *Phylloceras heterophyllum* (Sowerby, 1820), TV446; **c, d, e** - *Phylloceras heterophyllum* (Sowerby, 1820), TM461; **f** - *Phylloceras heterophyllum* (Sowerby, 1820), TU979; **g, h** - *Phylloceras heterophyllum* (Sowerby, 1820), TM473; **i** - *Phylloceras heterophyllum* (Sowerby, 1820), TM509f; **j** - *Phylloceras heterophyllum* (Sowerby, 1820), TU143. Scale bar: 1 cm long.


a
b
c
d
e
f
g
h
i
j



Plate 2: a – Slab with gigantic specimen of *Phylloceras heterophyllum* (Sowerby, 1820), TI009, named Cornucopia, and several 10 cm sized dactylioceratids accumulated by stream close to the opening of the giant ammonites. Scale bar: 1 cm long.

bution within the Serpentinum, Bifrons, and Variabilis Chronozones, across both NW European (e.g. Joly 2000; Rulleau 2007) and Mediterranean (e.g. Di Cencio 2007) palaeogeographic provinces.

Order Ammonitida Fischer, 1882
Suborder Ammonitina Fischer, 1882
Superfamily Lytoceratoidea Neumayr, 1875
Family Lytoceratidae Neumayr, 1875
Subfamily Lytoceratinae Neumayr, 1875

Genus *Lytoceras* Suess, 1865

Discussion - *Lytoceras* is a cosmopolitan genus known from the Sinemurian (Lower Jurassic) to the Cenomanian (Upper Cretaceous) (Hoffmann

2015). Easily recognisable by its distinctive suture line—the lytoceratine type— and Hoffmann (2010, 2015) identifies several subgenera that group small-sized ammonites with a subcircular whorl section, namely *Derolytoceras* and *Trachylytoceras*. The latter subgenus encompasses all lytoceratids displaying the aforementioned characteristics and of Toarcian (Lower Jurassic) (Hoffmann 2010, 2015).

Subgenus *Trachylytoceras* Buckman, 1913

Type species – *Ammonites nitidus* Young & Bird, (1828: 256). Buckman (1913: pl. 86) illustrated specimen WM2547 as the holotype of the species. The holotype is stored at Whitby Museum (UK).

Discussion - *Trachylytoceras* is a subgenus of *Lytoceras* that encompasses numerous Toarcian sub rounded and small size lytoceratids with an ornamentation consisting of more or less prominent fine growth striae., ranging from the Serpentinum to the Bifrons zones. Géczy (1967) also assigned the species *Lytoceras sepositum* Meneghini, 1875 to subgenus *Trachylytoceras*. These two species share a rather rounded whorl section and a similar degree of whorl involution, but they differ in their ornamentation: sinuous and prorsiradiate in *L. (T.) nitidum*, as opposed to the less pronounced and more radial ornamentation of *L. (T.) sepositum*.

Lytoceras (*Trachylytoceras*) *nitidum* (Young & Bird, 1828)

(Pl. 3, figs. c, d, e, f)

* 1828 *Ammonites nitidus* Young et Bird, p. 256; pl. 86.

1829 *Ammonites balteatus* Phillips, p. 163, pl. 12, fig. 17.

1835 *Ammonites balteatus* Phillips, Phillips, p. 135, pl. 12, fig. 17

1913 *Trachylytoceras nitidum* (Y. et B.), Buckman, pl. 86.

1983 *Trachylytoceras nitidum* (Y. et B.), Weitschat, p. 33.

1998 *Lytoceras* (*Trachylytoceras*) aff. *nitidum* (Young & Bird); Rulleau, p. 49 pl. 14, fig. 4

2015 *L.* (*T.*) *nitidus* (Young & Bird), Hoffmann, p. 10, fig. 7, 2a–b.

Holotype - *Ammonites nitidus* Young & Bird (1828: 256, pl. 86). Buckman (1913: pl. 86) illustrated specimen WM2547 as the holotype of the species. Howarth (1962) noted that WM2547 should be considered the reference specimen for identifying the species, despite the uncertainty surrounding its original status. Phillips established *Ammonites balteatus* in 1829 (p. 163, pl. 12, fig. 17), later designating the holotype in 1835 (p. 135, pl. 12, fig. 17). Upon examining the figured types, Howarth (1962) identified WM2547 as the specimen illustrated by Phillips (1835), thereby formally placing *Ammonites balteatus* in synonymy with *Lytoceras* (*Trachylytoceras*) *nitidum*.

Material - A single specimen was examined (MNHNL TV508).

Description - Evolute, planispiral serpenticone ammonite with the outer whorls resting upon the inner ones, covering only the ventral area. The whorl section is sub-oval to nearly sub-circular, slightly higher than wide. The flanks are gently rounded. The venter is also sub-rounded and relatively narrow. The umbilicus is wide and deep, bordered by high, rounded umbilical walls. Ornamentation consists of fine but well-defined ribs, not widely spaced, with a tendency to overlap along the flanks of the inner whorls. The ribs are weakly sinuous with a retroverse inclination and exhibit convexity in the direction of growth. They continue uninterrupted across the venter, where they become slightly concave. The shell is covered by a pseudoconch that almost entirely obscures the suture line. The suture is of the lytoceratine type, with short, stout, and highly frilled elements. The preserved body chamber spans just over half a whorl, though the peristome is not preserved.

Remarks - The studied specimen shows a strong resemblance to the figured type in Hoffmann (2015), although the latter displays more widely spaced ornamentation. The present specimen also closely resembles *L. ceratophagum* figured by Riegraf et al. (1984: pl. 2, fig. 5), from which it differs in having more sinuous ribbing. Arp et al. (2021: fig. 10.7) show—without description—a specimen that closely resembles the inner whorls of the present type, and which is referred to in that publication as *L. ceratophagum*. Finally, the specimen described herein bears a strong resemblance to that figured by Rulleau (1998: pl. 4, fig. 4).

Occurrence - The specimen examined in this study is associated with *Hildoceras lusitanicum* and likely originates from the Lusitanicum zonule (Sublevisoni Subchronozone, Bifrons Chronozone) confirming Hoffmann (2010, 2015) who reported *Lytoceras* (*Trachylytoceras*) *nitidum* from the NW European province (present-day England, France, and Northern Germany), within the Serpentinum Chronozone and the lower part of the Bifrons Chronozone.

Subfamily Alocolytoceratinae Spath, 1927

Genus *Alocolytoceras* Hyatt, 1900

Alocolytoceras dorcadis (Meneghini, 1875)
(Pl. 3, figs. a, b)

* 1875 *Lytoceras Dorcadis* n. sp. Meneghini, p. 107

1906 *Lytoceras dorcadis* Meneghini; Parish & Viale, p. 145; pl. 7, figs. 3, 4.

1931 *Lytoceras Dorcadis* Meneghini; Monestier, p. 10; pl. 7, figs. 1, 3, 4, 6, 7; pl. 9, fig. 10.

1967 *Alocolytoceras dorcadis* (Meneghini, 1867-81); Gèczy, p. 79; pl. 22, fig. 1; pl. 64, fig. 32.

v. 2007 *Alocolytoceras dorcadis* (Meneghini, 1875); Di Cencio, pl. 5, figs. 1-3, 7, 16, 17; pl. 6, figs. 2-4, 7, 9, 12, 14, 15, 17; pl. 7, figs. 1, 3, 6, 9, 13, 14

2008 *Alocolytoceras dorcadis* (Meneghini, 1875), Bourillot, Neige, Pierre & Durlet, p. 600, pl. 1, figs. 1–3.

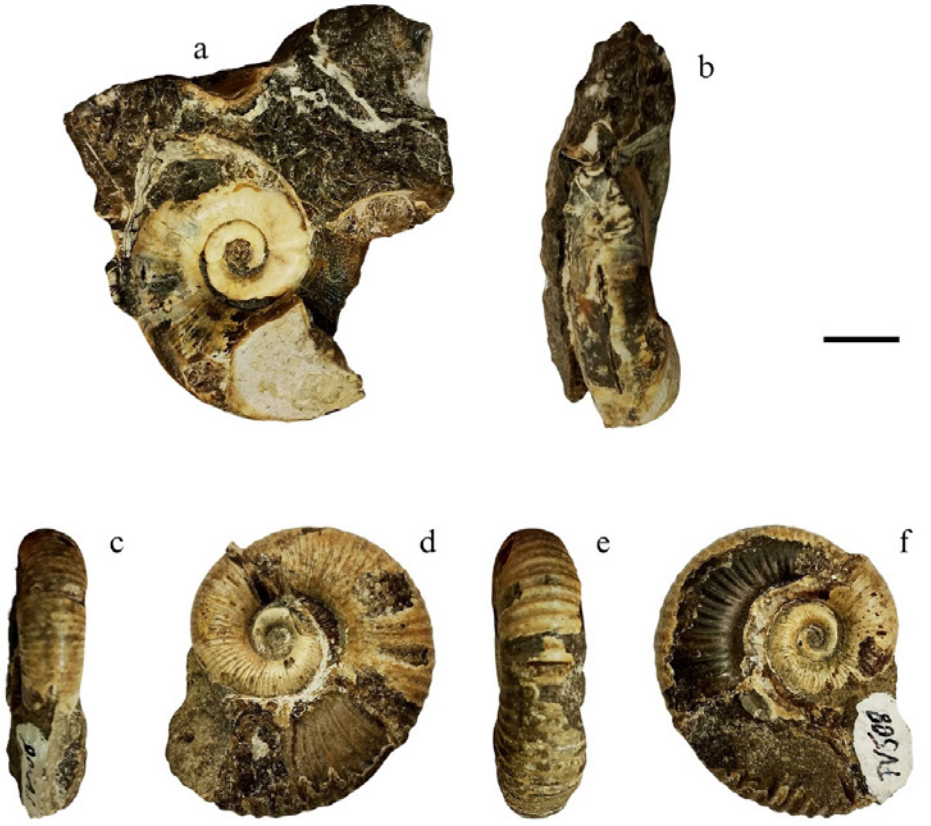


Plate 3: a, b - *Alocolytoceras dorcadis* (Meneghini, 1875), TM471; c, d, e, f - *Lytoceras (Trachylytoceras) nitidum* (Young & Bird, 1828), TV508. Scale bar: 1 cm long.

Holotype - The species has been established on *Lytoceras dorcadis* by Meneghini (1875: 107).

Material - A single specimen was examined (MNHNL TM471).

Description - Evolute, planspiral shell with moderately rapidly expanding whorls that barely overlap the underlying ones. The whorl section is sub-rounded with rounded flanks. The venter is broad and smooth. The umbilicus is wide and relatively deep, bordered by high, rounded umbilical walls. Ornamentation consists of regularly spaced constrictions occurring approximately every quarter-whorl along the coiling. These constrictions are sub-radial, slightly sinuous, apparently. The milky-white pseudo-conch is preserved; it exhibits dense, fine growth striae arranged parallel to the constrictions. The siphuncle is also preserved and prominently visible on the venter. It is located ventrally, between the internal shell filling and the lower surface of the pseudo-conch, appearing as a thin, black tubular structure. The body chamber is not preserved. The suture line is of the lytoceratine type with well-developed elements. The external saddle (E) is broad and deep. The external lobe (ES) is well developed, especially towards the flank, and displays a highly frilled and floral appearance. The lateral lobe (L) is deep and strongly frilled, bifurcating at the base to form an accessory saddle. The first lateral saddle (SL_1) is very well developed and finely frilled. The third umbilical lobe (U_3) is also deep and well defined.

Remarks - The specimen examined here shows a perfect correspondence with the *Alocolytoceras dorcadis* types illustrated by Di Cencio (2007), by Bourillot et al. (2008) and by Hoffmann (2010, 2015). *Alocolytoceras dorcadis* differs from other species of *Alocolytoceras* by its more oval whorl section and the number of constrictions.

Occurrence - *Alocolytoceras dorcadis* is a cosmopolitan species reported from Morocco (Bourillot et al. 2008, Rosales et al. 2025), Germany (Riegraf et al. 1984), France (Monestier 1931), and Italy (Venturi & Ferri 2001; Di Cencio 2007). Its stratigraphic range extends from the Serpentinum Chronozone in the lower Toarcian to the Bonarellii Chronozone in the upper Toarcian (Di Cencio 2007; Bourillot et al. 2008).

Superfamily Eoderoceratoidea Spath, 1929
Family Dactylioceratidae Hyatt, 1867
Subfamily Dactylioceratinae Hyatt, 1867

Genus *Dactylioceras* Hyatt, 1867

Type species - The genus is established on *Ammonites communis* by Sowerby (1815: 10, pl. 107, figs 2, 3).

Discussion - *Dactylioceras* is a genus with worldwide distribution with the earliest occurrence possibly in the Spinatum Chronozone (upper Pliensbachian, sensu Howarth 2013), and particularly abundant in lower Toarcian strata, from the Tenuicostatum Chronozone to the Commune Subchronozone of the lower part of the Bifrons Chronozone (Howarth 2013; Rulleau et al. 2013). The earliest forms, historically classified as *Dactylioceras* (*Eodactylites*) *mirabilis*, mark the base of the Mirabilis Subchronozone in Central Italy (Faraoni et al. 1994), which defines the onset of the Toarcian Stage (Elmi et al. 1997; Di Cencio 2007; Satolli et al. 2018). *Dactylioceras* has been subdivided into three subgenera: *Eodactylites* Schmidt-Effing, 1972, for forms with widely spaced, bifurcating ribs from the base of the Toarcian; *Orthodactylites* Buckman, 1926, for forms with denser, more or less bifurcate ribbing from the Tenuicostatum and Serpentinum Chronozones; and *Dactylioceras sensu stricto*, for forms with spaced, bifurcate ribbing and a more compressed shell morphology, typical of the Serpentinum and Bifrons Chronozones. Kutygin & Knyazev (2000) consider only the genus *Dactylioceras* to be valid, arguing that a purely stratigraphic criterion is insufficient for a meaningful systematic subdivision. Di Cencio (2007) elevated *Eodactylites* and *Orthodactylites* to generic rank, while omitting *Dactylioceras s.s.*, which is absent from the Mediterranean Tethyan province of Central Italy. Pinna & Levi Setti (1971) reported the presence of *Dactylioceras* from Gola del Furlo (Central Italy). Rulleau et al. (2013) retain all three subgenera, whereas Howarth (2013) places *Eodactylites* in synonymy with *Dactylioceras*, retaining only the remaining two subgenera. Howarth (2013) also synonymises the subgenus *Microdactylites* with *Dactylioceras*, in contrast to Rulleau et al. (2013), who considers it valid. In the present work, the subdivision into subgenera as proposed by Rulleau et al. (2013) is retained. The *Dactylioceras* specimens examined herein can be distinguished from co-occurring *Nodicoeloceras* by the absence of

spines or tubercles associated with rib bifurcation and by their more compressed whorl section.

Subgenus *Dactylioceras* Hyatt 1867

Discussion - Within the *Dactylioceras* assemblage studied, four species have been identified, described here in order of whorl compression, from the most compressed to the most depressed: *Dactylioceras* (*Dactylioceras*) *holandrei* (d'Orbigny, 1844), *Dactylioceras* (*Dactylioceras*) *athleticum* (Simpson, 1855), *Dactylioceras* (*Dactylioceras*) *commune* (Sowerby, 1815), and *Dactylioceras* (*Dactylioceras*) *crassiusculum* (Simpson, 1855). Rulleau et al. (2013) note that distinguishing between *D.* (*D.*) *athleticum*, *D.* (*D.*) *holandrei*, and *D.* (*D.*) *commune* can be particularly challenging. In the present study, an attempt is made to identify meaningful differences that may assist those approaching these fossils by providing straightforward diagnostic criteria. All forms are spineless, with the exception of *D.* (*D.*) *crassiusculum*, which exhibits a tendency toward spine development.

Occurrence - All the species examined are common in the lower part of the Bifrons Chronozone. Some authors have even used these forms as subchronozonal markers and biohorizon indicators for the Subboreal paleogeographic province (Page 2003, 2004).

Dactylioceras (*Dactylioceras*) *holandrei* (d'Orbigny, 1844)

(Pl. 4)

* 1844 *Ammonites holandrei* d'Orbigny nov. sp. p. 330; pl. 105.

1971 *Dactylioceras holandrei* (d'Orbigny, 1842); Pinna & Levi Setti, pl. 3, fig. 17a, b.

2013 *Dactylioceras* (*Dactylioceras*) *holandrei* (d'Orbigny, 1845); Rulleau, Lacroix, Becaud & Le Pichon, p. 78; pl. 11, figs. 5-6, 8; pl. 12 figs. 3-4, 7, 9.

Holotype - *Ammonites Holandrei* has been instituted by D'ORBIGNY (1844: 330; pl. 105).

Material - A total of 121 specimens were studied (MNHNL TM123f, 408a, e, f, g, i, k, l, n, p, q, 423, 430, 438a, 504, 511a, TU114b, i, j, 120, 134a, 176c, d, f, 192, 241g, 309b, c, 407a, c, 408a, c, d, 411, 414, 428, 431b, 434, 448, 520, 522, 878a, c, d, e, f, g, h, 929a, b, c, d, e, f, g, h, i, 973a, c, d, 981a, b, c, e, f, g, h, i, j, k, TV021, 023, 089, 090a, b, c, d, e, g, i, j, 288a, 292b, 294a, 304, 318, 320c, d, 322a, b, 326b, 365, 509a, b, 510a, 522, 525, 553a, f, 560b, d, e, 563a, b, d, e, g, h, i, k, l, m, o, 566a, f, 567a, f, g, 568c, d, 824c).

Description - Evolute, planispiral shell with outer whorls covering only the ventral portion of the inner ones. The whorl section is compressed, ranging from sub-oval to sub-rectangular in shape, with flat flanks. The umbilical area is broad and flat, bordered by a prominent, rounded umbilical wall. The venter is narrow, rounded to sub-triangular, and crossed by ribs. The body chamber extends over more than three-quarters of a whorl. The peristome is simple, featuring a broad constriction that spans two ribs prior to the aperture. Ornamentation consists of primary and secondary ribs. Primary ribs are strong, relatively spaced, prorsiradiate, and slightly sinuous. Towards the aperture, rib spacing becomes narrower. Typically, each primary rib bifurcates into two secondary ribs, without the presence of fibulae or tubercles. In some cases, secondary ribs develop independently of primary ones. Secondary ribs are markedly prorsiradiate, and the angle formed at their junction with the primary ribs is often a diagnostic feature. Fragments of a pseudoconch are preserved and obscure portions of the suture line. The visible suture elements are large and well developed. The external saddle (ES) is incompletely exposed but exhibits a deep accessory lobe, with a relatively weakly developed inner side. The lateral lobe (L) is deep and indented; its outer margin is directed towards the venter, while the inner margin runs parallel to the coiling. The first lateral saddle (SL_1) is broad and marked by two deep accessory lobes. The second umbilical lobe (U_2) is short, poorly developed, and notched.

Remarks - *D.* (*D.*) *holandrei* closely resembles *D.* (*D.*) *athleticum*, and to a lesser extent *D.* (*D.*) *commune*.

Plate 4: **a** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TM430; **b** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TU414; **c** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TU448; **d, e** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TM423; **f** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TM504; **g** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TV318; **h** - *Dactylioceras (Dactylioceras) holandrei* (d'Orbigny, 1844), TU192. Scale bar: 1 cm long.


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However, it can be distinguished from these species by its more compressed shell, the greater sinuosity of the primary ribs, the pronounced angle at the bifurcation between primary and secondary ribs, and the strongly prorsiradiate nature of the secondary ribs. Pinna and Levi Setti (1971) reported the presence of *D. (D.) holandrei* from Italian localities; however, Rulleau et al. (2013) argued that this material does not belong to the species. Using the parameters adopted in the present study, the identification is confirmed.

Occurrence - *Dactylioceras holandrei* occurs in strata dated to the Sublevisoni to Tethysi zonules, corresponding to Sublevisoni Subchronozone, Bifrons Chronozone (Rulleau et al. 2013). It has been recorded from France, England, and Luxembourg and Italy.

Dactylioceras (*Dactylioceras*) *athleticum* (Simpson, 1855)

(Pl. 5)

* 1855 *Ammonites athleticus* Simpson, p. 102.

1912 *Dactylioceras athleticum* Simpson, Buckman, pls. 51a, 51b.

1920 *Dactylioceras subcommune* n. sp., Ernst, p. 287

1962 *Dactylioceras athleticum* (Simpson, 1855), Howarth, p. 409.

1968 *Dactylioceras athleticum* (Simpson, 1855), Lehmann, p. 50, pl. 17, fig. 1, 7, 11; pl. 18

1971 *Dactylioceras athleticum* (d'Orbigny, 1842); Pinna & Levi Setti, pl. 3, fig. 15a, b.

2002 *Dactylioceras athleticum* (Simpson), Kroger, p. 201, fig. 4.

2013 *D.* (*Dactylioceras*) *athleticum* (Simpson, 1855); Rulleau, Lacroix, Becaud & Le Pichon, p 29; pl. 9 figs. 3, 4; pl. 10; pl. 11 fig. 1

Holotype - The species was established by Simpson (1855: 102) based on material originating from localities near Whitby (UK). The holotype was illustrated by Buckman (1912: pl. 51a).

Material - A total of 127 specimens were studied (MNHNL TI005d, 008a, f, g, h, k, TM103, 123d, 125, 407g, 408b, d, o, 409d, e, 417, 419, 420a, b, 424, 426, 432f, 435, 438d, e, f, 445b, c, 462, 474, TU114c, d, e, 121, 134b, d, 176a, e, g, 185, 193, 398a, b, 399a, b, c, d, e, f, g, h, i, j, k, l, m, n, o, p, 405a, b, c, 409a, b, c, d, e, 418, 431a, 435, 420a, b, c, 425, 442, 450a, c, 453, 455a, c, d, e, 486, 526, 597b, 878b, 981d, 966a, TV090k, 292a, 295, 306, 317, 320b, 321, 326a, 510b, c, 524a, c, 556b, c, 560a, c, f, 563c, f, j, n, 565b, 566b, c, d, e, h, j, k, i, 567b, c, i, j, 872, 824, 875a, b, 877h).

Description - Evolute, planispiral shell in which the external whorls only partially cover the flanks of the preceding ones. The whorl section is sub-oval to sub-rectangular, laterally compressed, with flat flanks. The umbilical area is broad and flat, bounded by a conspicuous, rounded umbilical wall. The ventral area is narrow, rounded to sub-triangular in outline, and crossed by prominent ribs. The body chamber occupies approximately a full whorl. The peristome is simple, preceded by a pronounced constriction that affects two ribs. Ornamentation consists of both primary and secondary ribs. Primary ribs are robust, moderately spaced, rectiradiate, and slightly proverse. Rib spacing decreases towards the aperture. Typically, each primary rib bifurcates into two secondary ribs, without the presence of fibulae or tubercles. In some specimens, a secondary rib may develop posteriorly from another, resulting in three secondaries emerging from a single primary. Secondary ribs are slightly proverse and generally evenly spaced. As most of specimens preserve large part of, if not the entire, the body chamber, observation of the external portion of the suture line is not possible. The visible sutural elements are moderately developed. ES is only partially visible but displays a deep accessory lobe, while its inner side is poorly developed. L is deep and incised. SL_1 is broad and features two distinct accessory lobes, extending towards the umbilical region. U_2 is short, weakly developed and indented.

Remarks - *Dactylioceras* (*Dactylioceras*) *athleticum* closely resembles *D.* (*D.*) *holandrei*, from which it can be distinguished by its less acutely compressed section with a more rounded ventral area, by the inclination angle of the secondary ribs, and by the straighter, less proverse primary ribs. It differs from *D.* (*D.*) *commune* in possessing a more compressed whorl section.

Occurrence - Page (2004) defined a *D.* (*D.*) *athleticum* Biohorizon, originally proposed by Buckman



Plate 5: **a** - *Dactylioceras (Dactylioceras) athleticum* (Simpson, 1855); TM426; **b** - *Dactylioceras (Dactylioceras) athleticum* (Simpson, 1855), TM435; **c** - *Dactylioceras (Dactylioceras) athleticum* (Simpson, 1855), TM474; **d, e** - *Dactylioceras (Dactylioceras) athleticum* (Simpson, 1855), TM462; **f** - *Dactylioceras (Dactylioceras) athleticum* (Simpson, 1855), TM420a, b. Scale bar: 1 cm long.

(1930), marking the uppermost part of the Commune Subchronozone within the lower Bifrons Chronozone in the Subboreal paleogeographic province. *D.* (*D.*) *athleticum* occurs in association with *D.* (*D.*) *holandrei*. It has been reported from France, Germany, England, Hungary, Italy, and Luxembourg.

Dactylioceras (*Dactylioceras*) *commune* (Sowerby, 1815)

(Pl. 6)

* 1815 *Ammonites communis* Sowerby, p. 10, pl. 107, figs 2, 3.

1855 *A. crassibundus*, Simpson, p. 55.

1956 *Dactylioceras commune* (Sowerby); Arkell, pl. 33, fig. 4.

1957 *Dactylioceras commune* (Sowerby); Arkell et al., Treatise, p. L255, fig. 5).

1961 *Dactylioceras commune* (Sowerby); Dean, Donovan & Howarth, p. 481, pl. 72, fig. 5.

1962 *Dactylioceras crassibundum* (Simpson), Howarth, p. 115, pl. 16, fig. 7 a, b.

2013 *Dactylioceras* (*Dactylioceras*) *commune* (Sowerby), Rulleau, Lacroix, Becaud & Le Pichon, p. 78, pl. 7, figs 2-4, pl. 8, figs 1-2, pl. 9, figs 1-2, 5-6, pl. 13, figs 1-2

2014 *Dactylioceras* (*Dactylioceras*) *commune* (Sowerby, 1815), Kovacs p. 48, pl. 1, fig. 2.

2023 *Dactylioceras* (*Dactylioceras*) *commune* (J. Sowerby, 1815), Kovacs, Horváth-Kostka, Müller & Pálfy, p. 223, fig. 6.4.

Holotype - *Ammonites communis* Sowerby (1815: 10, pl. 107, figs. 2, 3). The lectotype was designated by Arkell (1956: pl. 33, fig. 4) and is housed at the British Museum under catalogue number 43895. It was refigured by Arkell et al. (1957: L255, fig. 5) and by Dean et al. (1961: pl. 72, fig. 5).

Material - Fifty specimens were examined (MNHNL TM408c, h, j, 418a, b, 425, 427, 432d, 438c, 439, 454, 457a, b, 501, 502, 506, 510, 511b, c, 513b, 514, TU109, 123, 134c, 141a, 176b, 184, 309a, 386a, b, 440, 450b, 465a, b, c, 597a, 977, TV284, 288b, 302, 325, 334a, 513, 566g, 567c, d, 866c, d, 874, 877d).

Description - Evolute, planispiral shell in which the external whorls only marginally cover the outer flanks of previous whorls. The whorl section is sub-circular to sub-quadrate in shape, with slightly rounded flanks. The umbilical area is broad and flat, bordered by a conspicuous, rounded umbilical wall. The ventral area is slightly rounded and ribbed. The body chamber spans approximately one full whorl. The peristome is simple and is preceded by a marked constriction involving two ribs before the aperture. In some specimens, it is possible to observe the interval between the final aperture and that of the preceding growth stage, with peristomal constrictions recurring every quarter of a whorl. Ornamentation consists of primary and secondary ribs. Primary ribs are strong, relatively spaced, and rectiradiate, though tending towards a retroradiate orientation. Ribs are initially slightly proverse but, during development, they curve backwards, creating a convex bulge against the direction of coiling. Rib spacing decreases towards the aperture. Typically, each primary rib gives rise to two secondary ribs, without fibulae or tubercles. Occasionally, a secondary rib is inserted posteriorly, resulting in the formation of three secondary ribs from a single primary. On the final whorls, secondary ribs are slightly proverse but generally cross the ventral area more or less transversely. The suture line is not entirely visible due to the exceptional preservation of specimens and their mode of deposition and preparation. The external lobe (E) is not preserved or recognisable. The external saddle (ES) is broad and well-developed, although its elements are rather stout, and it is enriched by a narrow but relatively deep accessory lobe. The saddle lies adjacent to the latero-ventral margin, with the portion to the left of the accessory lobe positioned on the flank. The lateral lobe is relatively narrow and sub-rectangular with slightly frilled sides, broadening at its base where it divides into three deep and sharply pointed branches. The first lateral saddle (SL_1) is well developed, with globose anterior terminations divided by a short accessory lobe. Umbilical elements are poorly developed and appear slightly retracted relative to the remainder of the suture line.

Remarks - *D.* (*D.*) *commune* can be distinguished from *D.* (*D.*) *athleticum* and *D.* (*D.*) *holandrei* by its less compressed section and by the secondary ribs, which are less proverse, often nearly transverse or even retroradiate. *D.* (*D.*) *commune* also differs from *D.* (*D.*) *crassiusculum* in being less depressed.

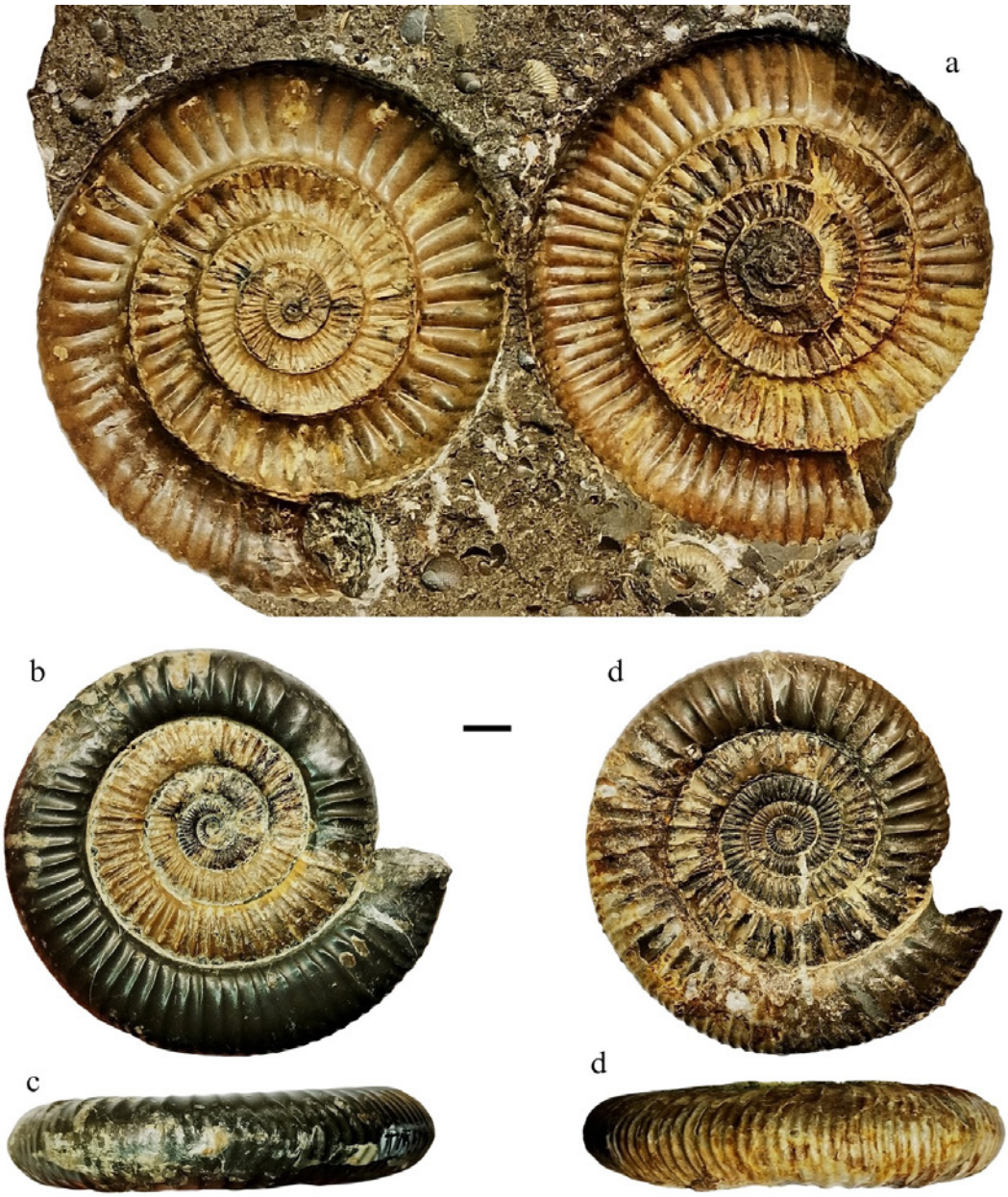


Plate 6: **a** - *Dactylioceras (Dactylioceras) commune* (Sowerby, 1815), TM457a, b; **b, c** - *Dactylioceras (Dactylioceras) commune* (Sowerby, 1815), TM506; **d, e** - *Dactylioceras (Dactylioceras) commune* (Sowerby, 1815), TM427. Scale bar: 1 cm long.

Occurrence - *D.* (*D.*) *commune* is a key species in the sub-Boreal province, where it defines the Commune Subchronozone, correlating with the Sublevisoni Subchronozone at the base of the Bifrons Chronozone. Page (2003, 2004) recognised a Commune Biohorizon, the second within the Commune Subchronozone of the lower Bifrons Chronozone for the sub-Boreal province (UK sense, Page 2003).

Dactylioceras (*Dactylioceras*) *crassiusculum* (Simpson, 1855)

(Pl. 7)

* 1855 *Ammonites crassiusculum* Simpson, p. 56.

1921 *Porpoceras crassiusculum* (Simpson); Buckman, pl. 209, fig. 1, 2.

1962 *Dactylioceras crassiusculum* (Simpson); Howarth, p. 116.

1997 *Dactylioceras* (*Dactylioceras*) *crassiusculum* (Simpson, 1855), Metodiev, p. 13; pl.1, fig. 3.

2013 *Dactylioceras* aff. *crassiusculum* (Simpson, 1855); Rulleau, Lacroix, Becaud & Le Pichon, p. 77; pl. 13, fig. 4.

Holotype - *Ammonites crassiusculus*, designated by Simpson (1855: 56). The holotype, catalogue number WM499, was illustrated by Buckman (1921: pl. 209).

Material - Thirteen specimens (MNHNL TM123b, 465, 466, 476, TU126, 408b, 965, TV342, 448, 515, 519, 520, 521).

Description - The shell is evolute and planispiral, with the outer whorl covering approximately one-third of the underlying whorls. The whorl section is sub-trapezoidal and depressed, being wider than high, with flat but flared flanks up to two-thirds from the umbilical wall. The umbilicus is relatively broad and shallow, bounded by a low, rounded umbilical wall. The venter is rounded and occupies the entire outer third of the lateral side. The body chamber spans more than three-quarters of a whorl, although the peristome is not preserved in any specimen. Along the body chamber, the whorl section becomes more compressed. Ornamentation consists of distinct primary and secondary ribs. Primary ribs arise on the lateral flanks, are proverse, straight or slightly sinuous, and clearly spaced. At the ventrolateral shoulder, they strengthen and typically bifurcate into two secondary ribs. Occasionally, a third secondary rib may appear adjacent to the bifurcation. Small spines are sometimes visible at the point of primary rib bifurcation. Secondary ribs curve proversely across the venter. On the body chamber, both primary and secondary ribs become less prominent and more widely spaced. The suture line displays well-developed elements: the external lobe (E) is deep and sharply incised, with a sub-triangular shape; the external saddle (ES) is indented and sub-rounded; the lateral lobe (L) is small and incised; the first lateral saddle (SL_1) is large and indented, bisected by an accessory lobe; the third umbilical lobe (U_3) is small in size.

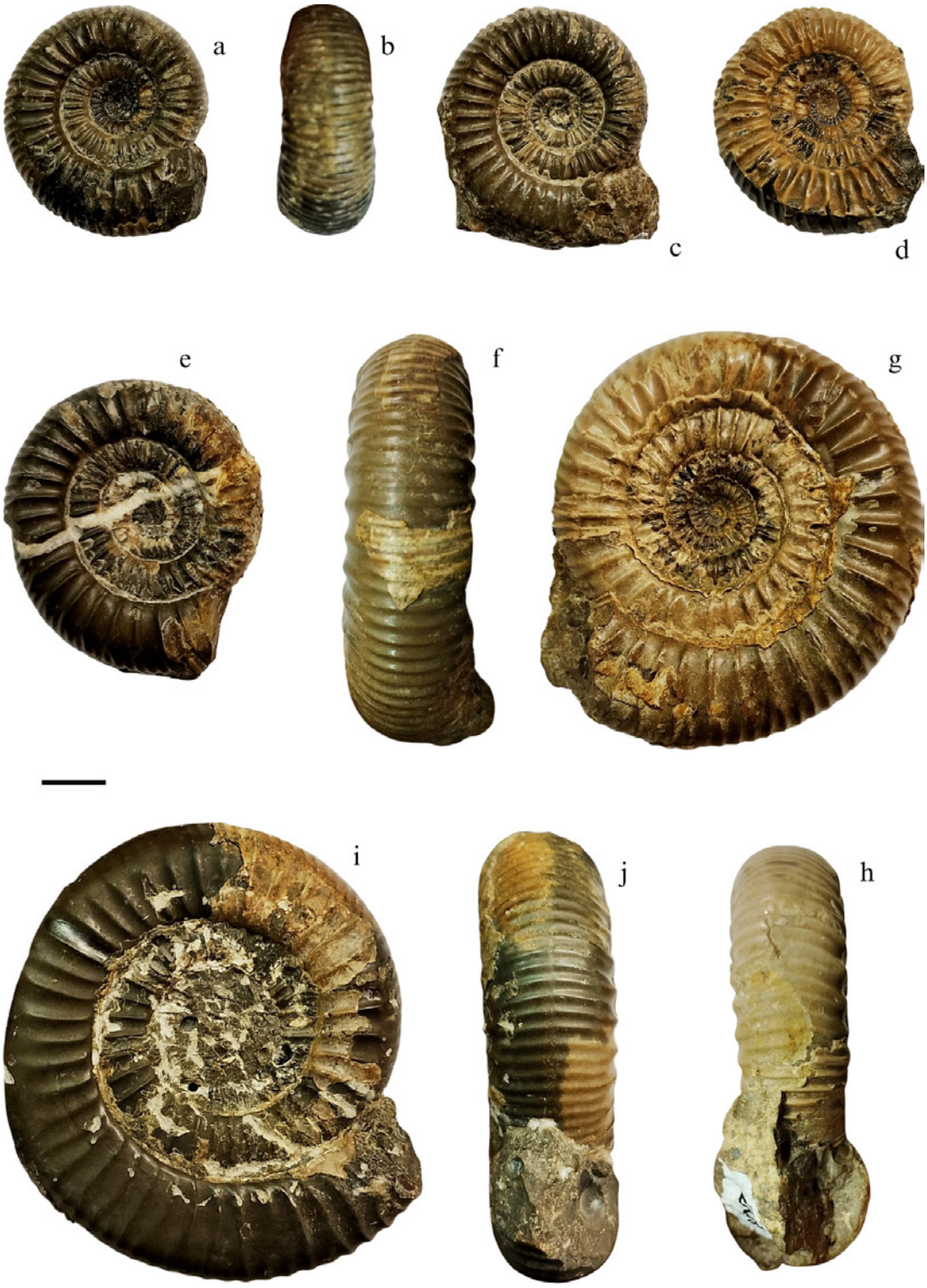
Remarks - Within the studied assemblage of *Dactylioceras* species, *D.* (*D.*) *crassiusculum* is the most depressed form, readily recognisable by its broader-than-high whorl section. Moreover, *D.* (*D.*) *crassiusculum* is also characterised by relatively small overall size compared to other *D.* (*D.*) species in the fossil association. In some specimens, there is a noticeable thickening of the rib segments at the bifurcation point, suggesting an incipient development of tubercles, possibly indicative of the future emergence of spines.

Occurrence - *Dactylioceras crassiusculum* occurs in association with all other taxa examined in this study. Page (2004) correlates *D.* (*D.*) *crassiusculum* with *D.* (*D.*) *commune* within the Commune Subchronozone for the Sub-Boreal paleogeographic province (UK).

Subgenus *Microdactylites* Buckman, 1926

Type species - The subgenus *Microdactylites* is established on *Ammonites attenuatus* Simpson (1855: 24), type material also for the species *D.* (*M.*) *attenuatus* (see below).

Plate 7: a, b - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TM476; c - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TM465; d - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TV342; e - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TM466; f, g, h - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TV520; l, j - *Dactylicoeras (Dactylioceras) crassiusculum* (Simpson, 1855), TV521. Scale bar: 1 cm long.


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Discussion - *Microdactylites* encompasses all small-sized forms that exhibit morphological features reminiscent of the subgenus *Dactylioceras*, namely evolute and compressed shells with sub-circular whorl sections and rounded flanks. These ammonites are characterised by a finer and more closely spaced ribbing pattern, composed of both primary and secondary ribs. They also display primitive traits, such as ribs that do not bifurcate but instead cross the whorl uninterrupted. Rulleau et al. (2013) recognise *Microdactylites* as a valid subgenus, whereas Howarth (2013) subsumes it within *Dactylioceras*. In accord with Rulleau et al. (2013) and observing the differences between the several *Dactylioceras* in the collection, *Microdactylites* is here retained as a subgenus of *Dactylioceras*.

Occurrence - *Dactylioceras* (*Microdactylites*) ranges stratigraphically from the Serpentinum to the Bifrons Chronozones and is documented in sediments from England, France, Germany, Italy, and Hungary.

Dactylioceras (*Microdactylites*) *attenuatum* (Simpson, 1855)

(Pl. 8)

* 1855 *Ammonites attenuatus*, Simpson, p. 54.

1926 *Microdactylites attenuatus* Simpson, Buckman, pl. 655.

1927 *Peronoceras praepositum* Buckman pl. 701.

1966 *Dactylioceras attenuatum* (Simpson) 1855, Fischer, p. 32, pl. 1, fig. 8; pl. 3, fig. 7

2002 *Dactylioceras attenuatus* (Simpson, 1855), Neige & Rouget, p. 767, figs 3a, 8a.

2017 *Dactylioceras* (*Dactylioceras*) *attenuatus* Buckman, 1926, Fauré, Cubaynes, Alméras, Lézin & Pellenard, pl. 2. Fig. 11.

Holotype - *Ammonites attenuatus* has been instituted by Simpson (1855: 54).

Material - Nine specimens (MNHNL TI008b, c, e, i, j, TM432a, b, 438b, TV877k).

Description - Evolute planispiral shell with whorls only partially overlapping the preceding ones. The whorl section is subcircular, and the shell exhibits slow growth. Flanks are gently rounded and converge toward a relatively rounded ventral region. The umbilicus is wide and shallow. The body chamber extends for slightly less than one full whorl. Ornamentation is defined by both primary and secondary ribs. Primary ribs, present on the flanks, are numerous, sinuous, and prosocline. They typically traverse the venter with minimal bifurcation. In the ventral area, ribbing is enriched by additional secondary ribs that originate independently from the ventrolateral margin and intercalate between the primaries.

Remarks - *Dactylioceras* (*Microdactylites*) *attenuatum* may initially be mistaken for the nucleus of another dactylioceratid species present within the same assemblage, such as *D.* (*D.*) *holandrei*, with which it shares the sinuous rib pattern—also noted by Hyatt (1872)—or with the early whorls of *D.* (*D.*) *athleticum* due to the rib count. However, it differs from the broader group in exhibiting markedly more rounded flanks. *D. (M.) attenuatum* exhibits ornamental characters typical of ancestral dactylioceratins from the base of the Toarcian [e.g. *D. (Eodactylites*) and *D. (Orthodactylites*)], such as the uniform spacing between primary and secondary ribs.

Occurrence - This species is recorded from the Sublevisoni Subchronozone, Lower Bifrons Chronozone. Fischer (1966) also places it in the Commune Subchronozone, correlated with Sublevisoni Subchronozone by Page (2003).

Genus *Nodicoeloceras* Buckman, 1926

Remarks - Many Dactylioceratid forms exhibiting tubercles, nodes, and spines along the whorl are grouped within *Nodicoeloceras*. The coiling morphology within this genus ranges from serpenticone to involute cadicone forms, encompassing both relatively compressed and more markedly depressed shells. *Nodicoeloceras* shows notable similarities to *Dactylioceras* (*Dactylioceras*) *crassiusculum*, which likewise begins to exhibit swellings along the ribs suggestive of incipient spination. *Nodicoeloceras* is a genus characteristically found within the Serpentinum and Bifrons chronozones.

Nodicoeloceras cf. *dayi* (Reynès, 1868)

(Pl. 9, figs. a, b, c)

* 1868 *Ammonites Dayi* n. sp. Reynès, pl. 5, fig. 7 a-d.



Plate 8: **a** - *Dactylioceras (Microdactylites) attenuatum* (Simpson, 1855), TI008b; **b** - *Dactylioceras (Microdactylites) attenuatum* (Simpson, 1855), TI008j; **c** - *Dactylioceras (Microdactylites) attenuatum* (Simpson, 1855), TI008e; **d** - *Dactylioceras (Microdactylites) attenuatum* (Simpson, 1855), TM438b; **e** - *Dactylioceras (Microdactylites) attenuatum* (Simpson, 1855), TI008c. Scale bar: 1 cm long.

1874 *Ammonites acanthopsis* (d'Orbigny), Dumortier, pl. 56, figs. 3-4.

1931 *Caeloceras* (*Peronoceras*) *millavense* n. sp. var. *crateriformis* n. n. Monestier, pl. I, fig. 7 et 13.

1931 *Caeloceras* (*Peronoceras*) *millavense* n. sp. var. *acanthopsis* d'Orb., Monestier, pl. 1, fig. 27, 29-30

1971 *Nodicoeloceras dayi* (Reynès), Guex p. 237; pl. 2, fig. la-c.

1976 *Nodicoeloceras dayi* (Reynès), Michon, p. 14; pl. 2, fig. 16.

1995 *Nodicoeloceras dayi* (Reynès), Rulleau, pl. 3, figs. 13-14.

2013 *Nodicoeloceras dayi* (Reynès), Fauré, p. 25; pl. 2, fig. 4.

Holotype - The species was established by Reynès (1868: pl. 5, fig. 7a–d). The holotype was subsequently re-illustrated by Guex (1971: 237).

Material - Two specimen (MNHNL TM464, 470).

Description - This is a small-sized, planispiral, moderately evolute shell in which the outer whorls cover approximately half of the underlying whorls. The whorl section grows relatively rapidly and is depressed, being significantly wider than high, with a sub-trapezoidal profile. The flanks are flat and converge towards the umbilical region. The umbilical area is relatively broad but markedly deep, bordered by a very low umbilical wall. The venter is broad, rounded, and occupies about half the whorl height. The body chamber is nearly three-quarters of a whorl in length, although the peristome is not preserved. The ornamentation consists of primary and secondary ribs. Primary ribs, located on the flanks, are well spaced, rectiradiate, and proverse. They terminate at the ventrolateral margin where they bifurcate into two, or rarely three, secondary ribs. Some secondary ribs also originate independently at the ventrolateral margin. At the bifurcation points, small circular tubercles are present,

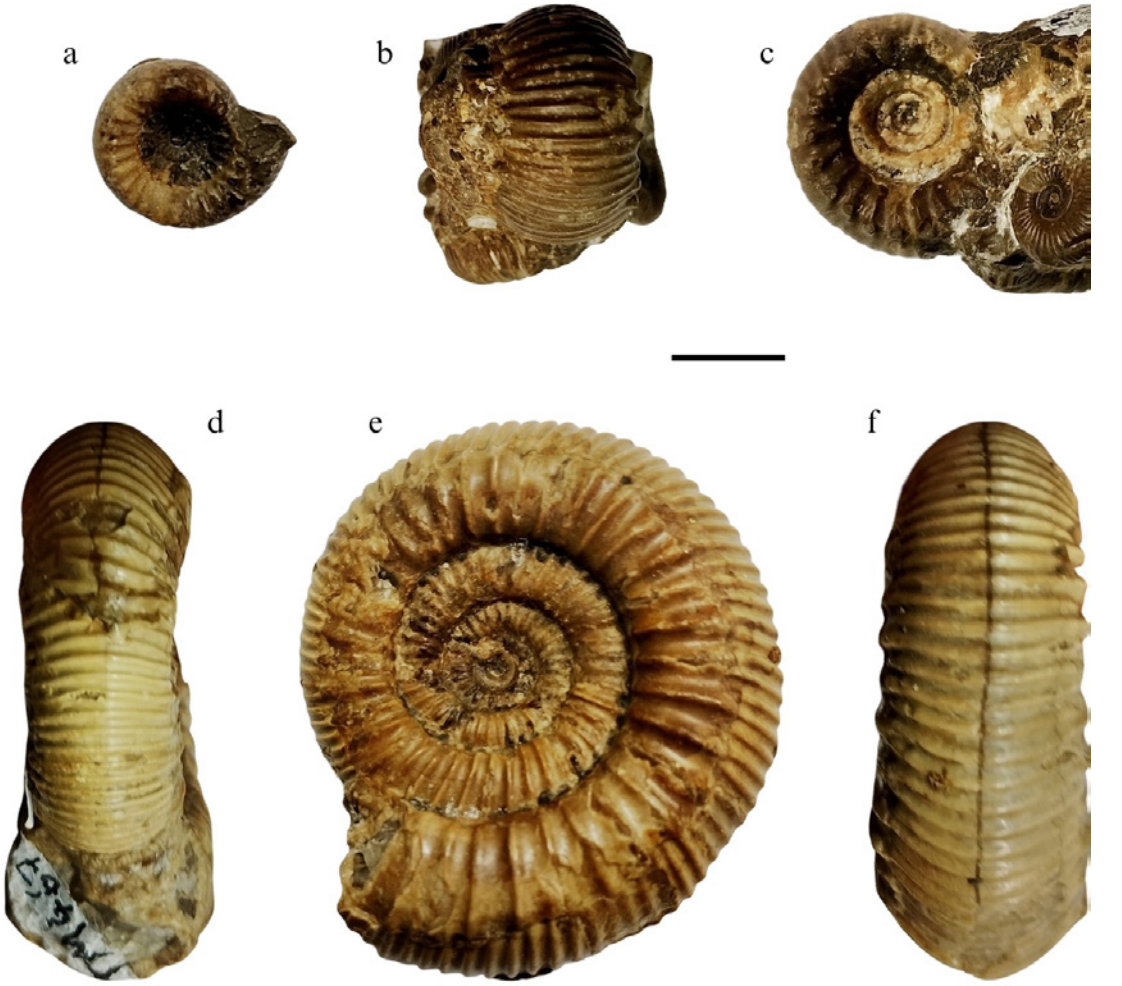


Plate 9: **a** - *Nodicoeloceras* cf. *dayi* (Reynès, 1868), TM464; **b, c** - *Nodicoeloceras* cf. *dayi* (Reynès, 1868), TM470; **d, e, f** - *Nodicoeloceras* sp., TM467. Scale bar: 1 cm long.

surmounted by minute spines which appear to continue the lateral trajectory of the secondary ribs. The secondary ribs are robust and traverse the venter transversely, connecting opposing flanks by way of the tubercles. The suture line is poorly preserved but clearly of dactylioceratine type, with short and weakly developed elements. The external lobe (E) is relatively deep and triangular with somewhat flared sides. The external saddle (ES) is globular and weakly developed. The lateral lobe (L) is well developed, sub-rectangular, and has parallel sides. All these elements are located in the ventral area. The umbilical margin of L coincides with the ventrolateral edge, placing the remaining suture elements within the flank. The first lateral saddle (SL_1) is well developed and sub-rectangular in shape. Beyond this, the umbilical elements are weakly developed and not readily identifiable.

Remarks - The specimen here studied are readily distinguishable from other dactylioceratines that are analyzed in this paper, due to their unique morphology within the studied palaeontological assemblage. However, given differences in the ornamentation of the secondary ribs compared with typical specimens and considering biostratigraphic constraints, the specimens analysed here are regarded as "confront" to *Nodicoeloceras dayi*. They differ from other depressed *Nodicoeloceras* species with sub-trapezoidal sections, such as *N. fontis* Guex, 1972 and *N. crateriforme* Monestier, 1931, by possessing a considerably broader transverse whorl section. While clearly assignable to *Nodicoeloceras*, the present specimens differ from those figured by Rulleau et al. (2013) in having more widely spaced secondary ribs on a more rounded venter. These specimens could potentially represent inner whorls of other species; therefore, extensive comparisons were undertaken.

Occurrences - In the literature, *Nodicoeloceras dayi* is typically dated to the upper part of the Bifrons Chronozone (e.g. Fauré 2013), near the transition to the Variabilis Chronozone, though other authors place it more generally within the Bifrons Chronozone. In the present study, the specimens clearly originate from the lower Bifrons Chronozone. Due to the limited number of specimens and stratigraphic considerations, the material is here referred to as *Nodicoeloceras* cf. *dayi*.

Nodicoeloceras sp.

(Pl. 9, figs. d, e, f)

Material - A single specimen (MNHNL TM467).

Description and remarks - This is a moderately evolved planispiral ammonite in which the outer whorls cover approximately half of the preceding ones. The coiling nevertheless extends over the outer region, which appears rather rounded and occupies about half of the flank. The umbilicus is relatively wide and shallow, bordered by a low umbilical wall. The whorl section is sub-circular, with gently rounded flanks. Ornamentation consists of primary and secondary ribs. The primary ribs are well-spaced, rectiradiate or slightly prorsiradiate, and not sinuous. Near the latero-ventral margin, the primary ribs bifurcate or trifurcate into secondary ribs. The fibulae are approximately half the length of a primary rib. At the point of bifurcation, swellings can be observed on the primary ribs, resembling small fibulae elongated parallel to the rib, acute, robust, yet lacking a spiny character. The secondary ribs are well-defined and slightly convex in the direction of coiling. Some arise from a primary rib, while others originate at the latero-ventral margin. The fossil is entirely covered by a pseudo-shell, preventing observation of the suture line. The specimen can confidently be assigned to *Nodicoeloceras*, owing to the regular presence of fibulae (visible in lower part of pl. 7 fig. c) at the transition between primary and secondary ribs. However, the morphology does not allow for a secure specific attribution, at least not at this stage.

Superfamily Hildoceratoidea Hyatt, 1867
Family Hildoceratidae Hyatt, 1867
Subfamily Harpoceratinae Neumayr, 1875
Genus *Harpoceras* Waagen, 1869

Subgenus *Maconiceras* Buckman, 1926

Type species - Buckman (1926: pl. 684) designated as type species of the subgenus the specimen he referred to as *Maconiceras vigoense*. However, the illustrated specimen was the same as that previously studied by Lissajous (1906: 28–29, pl. 1, figs. 5, 5a) under the name *Harpoceras* (*Maconiceras*) *soloniacense*.

Discussion - This subgenus includes all those small-sized harpoceratins whose general

morphology closely resembles that of *Harpoceras*: moderately involute coiling, falcoid ribs, and a keeled but unsulcate venter, although with significant distinctions. The ornamentation is defined by a peculiar costulation consisting of sparse, proverse, sub-falcoid ribs, alternated with mostly weakened ribs that nonetheless remain visible as concave traces along the ventrolateral margin. In the inner whorls, the falcoid character is lost, and the ribs appear sinuously proverse. Rib overlap is also observed, with some ribs fading out in the periumbilical area and others becoming more prominent. This type of ribbing justifies the assignment of such ornamented species to a subgenus distinct yet related to *Harpoceras*: *Maconiceras*. Bécaud (2006) noted the association of large harpoceratins belonging to *Harpoceras* with smaller and rarer specimens displaying slightly different ornamentation. Gabilly (1976) was the first to formally erect the name *Maconiceras* at the subgeneric level to distinguish the emended subgenus *Harpoceras*. While Howarth (1992, 2013) considered *Maconiceras* a junior synonym of *Harpoceras*. By contrast, Neige & Rouget (2002) raised *Maconiceras* to the rank of full genus. Lacroix & Le Pichon (2011) recognised a "*Maconiceras* stage" in certain illustrated forms.

Harpoceras (*Maconiceras*) *soloniacense* (Lissajous, 1906)

(Pl. 10)

* 1906 *Grammoceras soloniacense* Lissajous, p. 28, 29, pl.1, figs 4-6.

1927 *Maconiceras soloniacense*, Buckman, pl. 721.

2002 *Maconiceras soloniacense* (Lissajous, 1906), Neige & Rouget, p. 770, fig. 3d.

2006 *Harpoceras* (*Maconiceras*) aff. *soloniacense* (Lissajous, 1906), Becaud p. 66, pl. 3, figs. 3a-c.

2013 *Maconiceras soloniacense* (Lissajous, 1906), Fauré, p. 29, pl.3, fig. 4.

2014 *Maconiceras soloniacense* (Lissajous, 1906), Bardin, Rouget, Benzaggagh, Fürsich & Cecca, p. 26, fig13b, e, f.

Holotype - *Grammoceras soloniacense* Lissajous (1906: 28–29, pl. 1, figs. 5, 5a), established on a microconch specimen, later illustrated as lectotype by Buckman (1926: pl. 684).

Material - Six specimens (MNHNL TM418, 463, 469, 513a, 408m, 966b).

Description - The shell is moderately involute planispiral, with the outer whorls covering more than two-thirds or nearly the entirety of the inner ones. Whorl expansion is relatively rapid, and the cross-section is sub-lanceolate, with flat flanks converging towards a narrow, sub-rounded venter. The venter is marked by a pronounced keel. The umbilicus is shallow and almost entirely concealed by the final whorl; in more mature forms, it is bordered by high, vertical umbilical walls. In the inner whorls, ornamentation consists of fine, visibly sinuous and proverse ribs, only weakly falcoid. Rib overlaps are present: some ribs fade near the periumbilical zone, while others are reinforced. In the outer whorls, ornamentation evolves into moderately proverse, falcoid, robust ribs alternating with more evanescent ones, mostly visible only on the outer shell margin. Intercalations are evident between singular proverse falcoid ribs and fainter ribs, or as instances of rib capture where strong ribs incorporate successive weaker ones. This results in an apparent rib fasciculation, especially on the inner flanks, where ribs appear nearly fused. Isolated and obsolete ribs are also observable in the outer portion. The body chamber extends for just under two-thirds of a whorl and terminates in a peristome that mirrors the rib pattern—sinuous and proverse—with a prominently keeled venter. The suture line is of harpoceratine type, with multiple elements; however, due to the presence of a pseudoshell and the small size of the specimens, a complete description is not possible. The external lobe (E) is short and flared, enriched by a small accessory saddle (A). The external saddle (ES) is well developed, also flared and adorned with conspicuous denticulations, including a small but deep accessory lobe. The lateral lobe (L) is well-formed, broad and deep, terminating in seven denticulate endings. The first lateral saddle (SL_1) is weakly developed with minor frilled ornamentation, as are the subsequent lateral saddles. The umbilical lobe (U_3) is relatively deep, about half the height of SL_1, and ends in three denticulations, following the general direction of the coiling. U_2 is about half the length of U_3 and also follows the coiling direction.

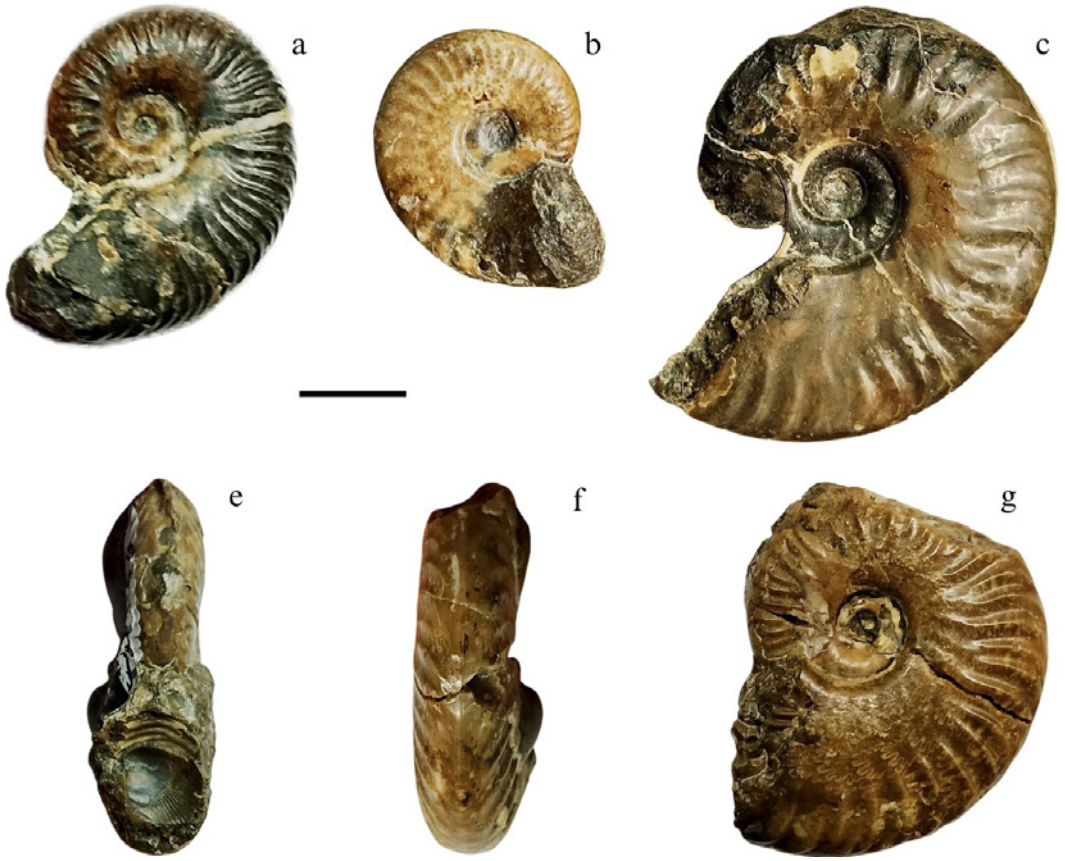


Plate 10: a - *Harpoceras (Maconiceras) soloniacense* (Lissajous, 1906), TM463; b - *Harpoceras (Maconiceras) soloniacense* (Lissajous, 1906), TM418b; c - *Harpoceras (Maconiceras) soloniacense* (Lissajous, 1906), TM513; d, e, f, - *Harpoceras (Maconiceras) soloniacense* (Lissajous, 1906), TM469. Scale bar: 1 cm long.

Remarks - The size of the specimens, together with the ornamentation characterised by falcoid to sinuous ribs that are variably spaced and differently accentuated, allows the material to be determined without any doubt as belonging to *Harpoceras (Maconiceras) soloniacense*. One specimen, TM463, slightly diverges from the diagnosis, displaying subtly different ornamentation at comparable diameters—features that are nonetheless present in the inner whorls of other specimens.

Occurrence - *Harpoceras* (*Maconiceras*) *soloniacense* occurs within the Serpentinum and Bifrons Chronozones of the NW European paleogeographic province. Bardin et al. (2014) figures some specimen from Mirabile Subchronozone (Polimorphum Chronozone, base of Toarcian for the Mediterrean province) of Morocco.

Subfamily Hildoceratinae Hyatt, 1867

Genus *Hildoceras* Hyatt, 1867

Hildoceras lusitanicum Meister, 1913
(Pl. 11)

* 1913 *Hildoceras bifrons* (Bruguière) var. *lusitanica* Meister; p. 548, pl. 12, fig. 3.

1930 *Hildoceras bifrons* (Bruguière) var. *crassa* Mitzopoulos, p. 45, pl. 4, fig. 7.

1992 *Hildoceras lusitanicum* Meister; Howarth, p. 181; p. 183, fig. 42; pl. 34, fig. 7; pl. 35, figs. 1-4; pl. 36, figs 1-3.



Plate 11: a, b - *Hildoceras lusitanicum* Meister, 1913, TM475; c - *Hildoceras lusitanicum* Meister, 1913, TM433; d - *Hildoceras lusitanicum* Meister, 1913, TM407, block with several almost complete specimen in a paviment-like assemblage; e, f - *Hildoceras lusitanicum* Meister, 1913, TM503; g - *Hildoceras lusitanicum* Meister, 1913, TM 509e; h, i, j - *Hildoceras lusitanicum* Meister, 1913, TM460. Scale bar: 1 cm long.

1996 *Hildoceras lusitanicum* Meister; Ridente, p. 180, pl. 1, figs. 7-10; pl. 2, figs. 1-10; pl. 3, figs. 1-8.

2007 *Hildoceras lusitanicum* Meister; Rulleau, p. 71; p. 72, figs. 18/7, 18/8; pl. 22, fig. 1a, b.

v. 2007 *Hildoceras lusitanicum* Meister, 1913, Di Cencio, pl.18, fig. 1-5, 7, 8, 10, 11, 14, 16, 18, 21; pl. 19, figs. 1-22; pl. 20, figs. 1-25.

Holotype - *Hildoceras bifrons* (Bruguière) var. *lusitanica* Meister, 1913. This species was established by Meister (1913: 548, pl. 12, fig. 3) based on a specimen originating from Lower Toarcian strata in Marmeleira, Portugal.

Material - A total of 67 specimens (MNHNL TI005a, e, f, g, TM101, 122, 123c, d, 407a, b, c, d, e, f, 409a, b, c, 432c, e, g, 433, 460, 475, 503, 509b, d, e, TU101, 140, 141b, c, f, 230, 296, 310, 401a, b, 403, 406a, b, 452, 521, 937a, 963, 970, 973b, TV161, 312b, 317, 320a, 323, 334b, c, 345, 437, 445, 511, 553b, c, d, e, 568a, 877a, e, f, g, i).

Description - The shell is evolute and planispiral, with the outer whorls covering less than one-third of the preceding whorl. Its cross-section ranges from sub-rectangular to sub-quadrate, with nearly flat flanks that show slight convergence towards the outer region, particularly from the outer third onwards. The venter is broad, bearing three distinct keels separated by two moderately shallow grooves. The umbilicus is relatively wide and moderately deep, delimited by tall, sub-rounded walls inclined at a modest angle. The body chamber spans two-thirds of a whorl and maintains the same ornamentation as the phragmocone. The peristome displays an elongation along the umbilical wall, lateral lappets aligned with the convex portions of ribs, and a continuation of the keels and ventral grooves. Ornamentation consists of ribs that range from radial to slightly retroverse, particularly on the inner whorls. These ribs are subtly sinuous, and their concave portions are well defined, whereas their convex parts are subdued, imparting a smoother appearance to the inner half of the flanks. A pseudo-groove may be observed along the flanks, corresponding to the smoothed convex portions of the ribs, likely resulting from alternating depressions between rib crests. In certain specimens, remnants of a thin pseudo-shell (1–1.5 mm thick) are preserved. This layer replicates the ornamentation of the fossil surface and retains distinct growth striae. These striae parallel the rib pattern, and in some specimens, particularly on the terminal part of the body chamber, the ribs become faint, leaving only growth striae to indicate their former presence. The suture line comprises simple yet well-developed elements: the external lobe (E) is broad, distinctly formed, and accompanied by an accessory triangular saddle (A). The external saddle (ES) is very wide, indented, and contains an accessory lobe; its internal branch extends further than the external one. The lateral lobe (L) is deep, clearly defined, and terminates in five pointed projections. The first lateral saddle (SL_1) is prominent, slightly longer than ES, indented, and bears an accessory lobe. Its internal branch is shorter than its external branch, from which the umbilical portion of the suture line originates. This umbilical section displays alternating lobes and broad, coarse saddles. Two lobes and a single saddle are generally discernible within this portion.

Remarks - The specimens identified as *Hildoceras lusitanicum* closely resemble those attributed to *Hildoceras sublevisoni* but differ in having a less elevated, flatter umbilical wall and an ornamentation pattern marked by a smoothed convex zone on the inner flanks. Furthermore, *H. lusitanicum* exhibits a pseudo-groove occasionally visible along the flanks. In contrast to members of the *Hildoceras bifrons* group (*H. apertum*, *H. bifrons*, *H. angustisiphonatum*, and *H. semipolitum*), *H. lusitanicum* lacks a consistently developed lateral groove extending throughout the entire whorl. According to Ridente (1996), a lateral groove appears in *H. lusitanicum* from the final volution onwards, and in progressively younger specimens it initiates earlier in the coiling; however, a continuous lateral groove throughout the shell is never present.

Occurrence - *Hildoceras lusitanicum* is commonly found at the upper part of the Sublevisoni Subchronozone (Lusitanicum zonule), Bifrons Chronozone, within both NW European and Mediterranean paleogeographic provinces.

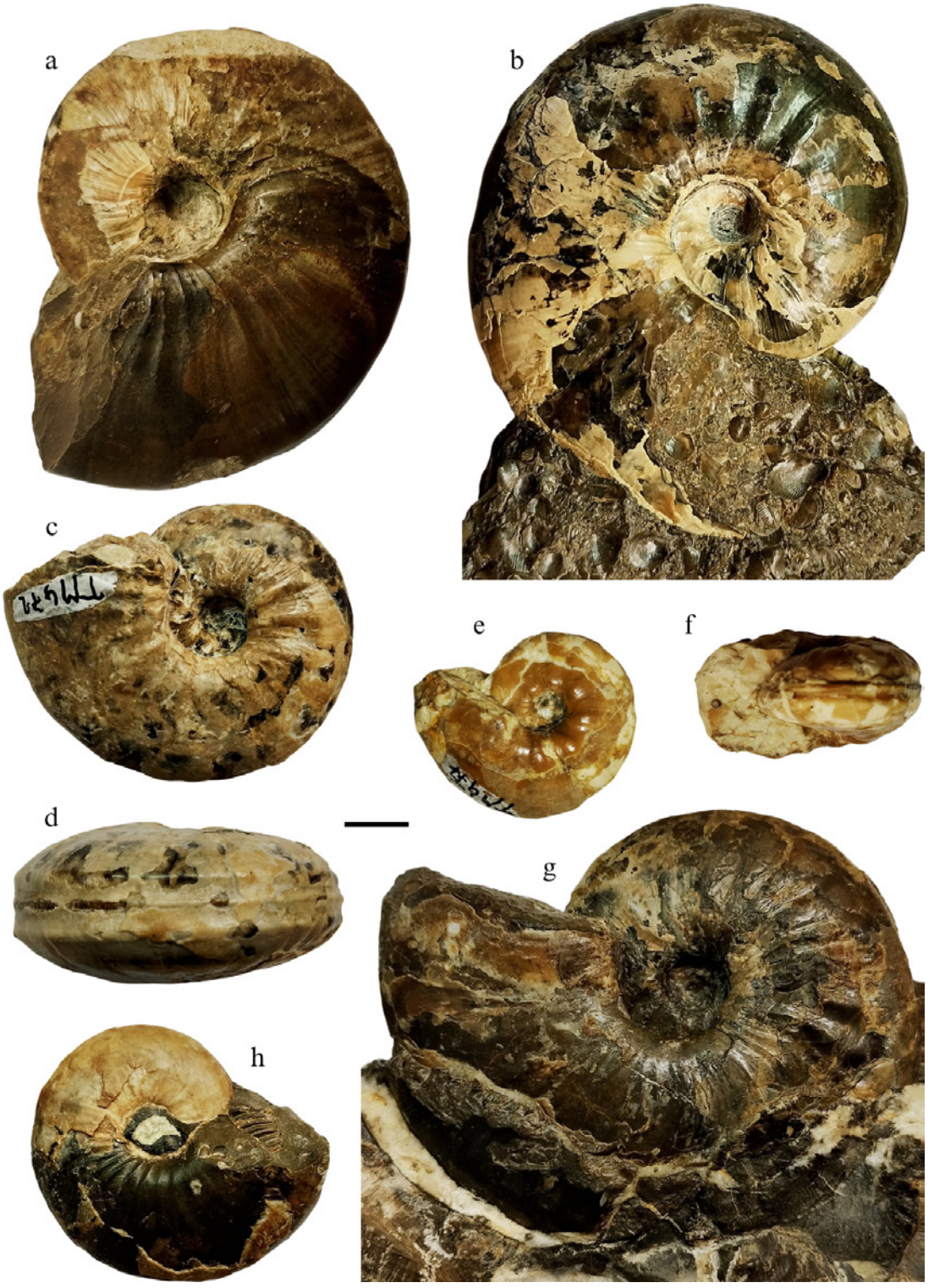
Subfamily Bouleiceratinae Arkell, 1950

Genus *Frechiella* Prinz 1904

Type species - The species has been established on *Ammonites subcarinatus* by Young & Bird (1822: 255, pl. 12, fig. 7).

Frechiella subcarinata (Young & Bird, 1822) (Pl. 12)

* 1822 *Nautilus subcarinatus* nov. sp. Young et Bird, p. 255, Pl. 12, Fig. 7.


a
b
c
e
f
d
g
h

1921 *Frechiella subcarinata* (Y. et B.), Monestier, p. 232, 234.

1931 *Frechiella subcarinata* (Y. et B.), Monestier, p. 14 ; Pl. 7, Fig. 2 ; Pl. 9, Fig. 3.

1971 *Frechiella subcarinata* (Y. et B.), Gabilly et al.,p. 606.

1972 *Frechiella subcarinata* (Y. et B.), Guex, p. 619.

1984 *Frechiella subcarinata* (Y. et B.), Maubeuge, p. 94, Figs. 63 et 64.

1992 *Frechiella subcarinata* (Y. et B.), Howarth, p. 157; Pl. 29, Figs. 4–7.

2001 *Frechiella subcarinata* (Y. et B.), Rulleau, Elmi & Thevenard, Pl. 10, Fig. 3.

2003 *Frechiella subcarinata* (Young & Bird, 1822), Rulleau, Becaud & Neige, figs. 13 (2,3,5), 14 (1)

Holotype - *Nautilus subcarinatus* Young & Bird, (1822: 255, pl. 12, fig. 7). The holotype, catalogue number WM63, was re-illustrated by Buckman (1910: pl. 23).

Material - Eight well-preserved specimens (MNHNL LO109, TM108, TU128, 913, TV319-01, 02, 03, 383).

Description - The shell is involute and planispiral, with the outer whorls almost completely overlapping the preceding ones. The cross-section is sub-trapezoidal, varying in compression, and characterised by rounded flanks. The greatest width of the whorl lies near the umbilical wall, from which the flanks begin, curving gently yet tending towards the external area. Some specimens are relatively robust, with a whorl width-to-height ratio (s/h) greater than 1, whereas others are more compressed, with s/h < 1. A progressive decrease in s/h is observed with increasing diameter, indicating a tendency towards compression as *Frechiella subcarinata* matures. The venter is broad, bearing three distinct keels separated by two grooves. In certain specimens, these grooves are diminished or absent, producing a triangular-shaped ventral area, with flat, sloping regions between the lateral and median keels, particularly in the outer whorls. The umbilicus is deep and bordered by high, prominent, rounded walls. The degree of involution varies: the umbilical diameter-to-outer diameter ratio (o/d) ranges from a minimum of 0.087 in the most involute forms to a maximum of 0.275 in specimens with a broader umbilicus. The body chamber extends beyond half a whorl, although the aperture is not preserved in any specimen. Ornamentation displays marked ontogenetic variability, with distinct ornamental phases along the coiling. At the smallest diameters, ornamentation is dominated by peri-umbilical swellings or bulges, elongated, slightly concave, and sub-radial in orientation. These swellings carry numerous fine growth striae or delicate sinuous costellae, aligned in the same direction. With increasing diameter, the swellings elongate, developing into prominent ribs that arise concavely from the umbilical wall and extend radially, becoming progressively sinuous along the flanks. In later whorls, the ribs thin, displaying a tendency towards bundling (fasciculation) and differentiation into primary and secondary ribs. Many specimens retain a thin pseudo-shell exhibiting the same ornamental features, additionally marked by growth striae. The suture line is pseudoceratitic, with primitive, weakly ornamented elements. The external lobe (E) is narrow and lies within the ventral grooves. The external saddle (ES) is broad, slightly indented, and bears a well-developed accessory lobe. The lateral lobe (L) is wide, deep, and strongly indented at its base. The first lateral saddle (SL_1) is broad, coarsely formed, and poorly ornamented. The umbilical portion of the suture line is represented by a small, weakly developed lobe.

Remarks - All examined material is attributed to *Frechiella subcarinata*. Both the specimens studied and data from the literature (e.g., Rulleau et al. 2003; Di Cencio 2007; Lacroix & Le Pichon 2011) indicate substantial intraspecific variability, as also suggested by the observed indices of involution and compression. Some forms exhibit a sub-triangular ventral area with barely defined grooves (e.g., TM108, TV383), while others display

Plate 12: **a** - *Frechiella subcarinata* (Young & Bird, 1822), TM108; **b** - *Frechiella subcarinata* (Young & Bird, 1822), LO109; **c, d** - *Frechiella subcarinata* (Young & Bird, 1822), TM472; **e, f** - *Frechiella subcarinata* (Young & Bird, 1822), TM477; **g** - *Frechiella subcarinata* (Young & Bird, 1822), TM509c; **h** - *Frechiella subcarinata* (Young & Bird, 1822), TV447. Scale bar: 1 cm long.

ornamentation resembling that of *F. venantii* (e.g., TV319-02, TM477). However, such characters occur in the inner whorls of specimens whose outer whorls show features typical of *F. subcarinata*. It is therefore inferred that an ontogenetic sequence exists in *F. subcarinata*, including a "*venantii* phase" and a subsequent "*kammerkarensis* phase" and, at the end, a "*subcarinata* phase".

Occurrence - *Frechiella subcarinata* co-occurs with species of *Hildoceras* (e.g., *H. sublevisoni*, *H. lusitanicum*) within the Sublevisoni Subchronozone (Lusitanicum zonule), lower Bifrons Chronozone.

5 Discussion: the *Dactylioceras* (*D.*) *holandrei* - *athleticum* - *commune* group

Three *Dactylioceras* species represented in the collection under study - *D. (D.) holandrei*, *D. (D.) athleticum*, and *D. (D.) commune* - exhibit very similar characteristics and are prone to confusing or erroneous classification, particularly when the preservation of the fossils is suboptimal. For this reason, it is necessary to attempt some clarification by compiling a list of diagnostic features for each species (Fig. 2). Hyatt (1872) was already aware of the close affinity among the three species of *Dactylioceras* (*Dactylioceras*) and particularly highlighted the marked resemblance between *D.* (*D.*) *commune* and *D.* (*D.*) *holandrei*, the latter being distinguished primarily by its greater degree of shell compression. The species *D.* (*D.*) *holandrei* and *D.* (*D.*) *athleticum* are also morphologically very similar, and numerous authors have noted the difficulty in differentiating them clearly (Fischer et al. 1994, Rulleau et al. 2013). However, thanks to the extensive material available for this study - comprising specimens in various states of preservation and completeness - it has been possible to establish diagnostic criteria that facilitate the distinction of these forms, even in the field during detailed palaeontological or biostratigraphic surveys. The first to propose the notion of a "*holandrei–athleticum* group" was Fischer et al. (1994). Given the close similarity and the co-occurrence of both species within the strata of the Lusitanicum Subchronozone of the Bifrons Chronozone, it becomes evident that they should be considered together. Nonetheless, certain

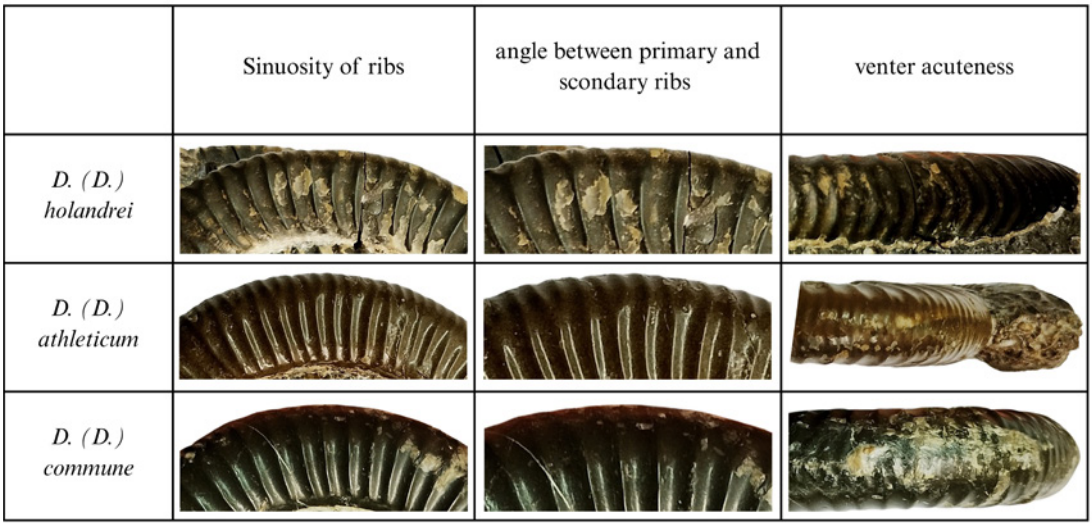


Fig. 2: Summary scheme of the differences among the species *D. (D.) holandrei, D. (D.) athleticum and D. (D.) commune*. It can be observed in the first column that the sinuosity of the ribs decreases from top to bottom. The angle between the primary and secondary ribs is clearly visible in *D. (D.) holandrei*, whereas it is only faintly indicated in the other two species. Finally, the third column shows that the outer area is more acute in *D. (D.) holandrei,* while it is less so, with a more circular whorl section, in the other two specimens. The compared types have already been illustrated, respectively in pl. 4 fig. g (TV318), pl. 5 fig. a (TM426) and pl. 6 fig. b (TM506).

distinguishing features can still be identified. Through comparison of the numerous specimens at hand, it has been possible to recognise subtle yet significant morphological differences that allow *D.* (*D.*) *holandrei* to be differentiated from *D.* (*D.*) *athleticum*. This chapter aims to synthesise those differences for comparative purposes. For completeness, the diagnostic features of *D.* (*D.*) *commune*, which is somewhat more distinct, are also included. Below is a summary of the main diagnostic features:

- *D.* (*D.*) *holandrei* is characterised by a highly compressed shell with a tall, acute, and rounded venter. Primary ribs are widely spaced and slightly sinuous. At the point of bifurcation, where secondary ribs emerge, a distinct bifurcation angle is visible. Secondary ribs are markedly forward curved (proverse).
- *D.* (*D.*) *athleticum* possesses a shell less compressed than D. holandrei with a rounded but non-acute venter. The primary ribs are widely spaced, rectiradiate or slightly proverse, and not sinuous. The bifurcation angle is noticeable, and the secondary ribs are only slightly proverse.
- *D.* (*D.*) *commune* exhibits a shell with minimal compression, with an almost sub-circular or square cross-section and a moderately rounded venter. The primary ribs are rectiradiate or weakly proverse and widely spaced. The angle between primary and secondary ribs is subtle, and secondary ribs are only slightly proverse, nearly transverse.

The most reliable character for distinguishing *holandrei* from *athleticum* is the pronounced acuteness of the venter in *holandrei*, a feature evident both in the holotype illustrated by Rulleau et al. (2013) and in the lectotype designated by Fischer et al. (1994). Although *athleticum* also exhibits a rounded venter, it lacks the marked acuteness that is typical of *holandrei*.

6 Conclusion

A substantial number of specimens ascribed to only a few ammonite species from the lower part of the Bifrons Chronozone, in the lower Toarcian of Luxembourg, have been examined. Preservation within the fossil-bearing nodules has allowed the conservation of complete ammonite specimens, virtually frozen in time. This has enabled the development of a crucial discussion regarding morphological variability within one of the represented genera - *Dactylioceras* - which has led to a redefinition of the classificatory parameters of the taxa in question. The studied nodules represent snapshots of a marine seafloor, preserving information about the conditions that led to their formation. The work presented here focuses on the taxonomic characteristics of the most abundant fossils, e.g. the ammonites, but it constitutes only a first step towards studies aimed at understanding the dynamics that permitted nodule formation and their deposition within the enclosing lithotype.

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Belemnitida, Diplobelida and Octobrachia from the early Toarcian of Luxembourg: a local window on the coleoid cephalopod diversity in the aftermath of the Toarcian Oceanic Anoxic Event

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Keywords: Systematics, palaeobiodiversity, Coleoidea, Cephalopoda, Toarcian, black shales, T-OAE.

Abstract

Coleoid cephalopods are common fossils in the early Toarcian black shales of Luxembourg. Despite their widespread occurrence, little is known concerning their taxonomic diversity and stratigraphic range. The present catalogue focuses on a revision of the coleoid Belemnitida, Diplobelida and Vampyromorpha (Octobrachia) occurring in deposits dated from the early Toarcian Serpentinum Zone, in the aftermath of the Toarcian Oceanic Anoxic Event. 111 specimens have been studied and the taxonomic analysis revealed the presence of 7 belemnitid species, one diplobelid and 7 octobrachian species. The octobrachian and diplobelid taxa occur in the lower part of the Serpentinum zone (Exaratum Subzone), whereas the belemnites are rare in that interval and occur more frequently in the upper part of the Serpentinum Zone (Falciferum Subzone).

Schlüsselwörter: Systematik, Paläobiodiversität, Coleoidea, Cephalopoda, Toarcium, bituminöse Schiefer, T-OAE.

Zusammenfassung

Kopffüßer der Unterklasse Coleoidea sind häufige Fossilien in den bituminösen Schiefern des frühen Toarcium Luxemburgs. Trotz ihres weit verbreiteten Vorkommens ist nur wenig über ihre taxonomische Vielfalt und stratigraphische Verbreitung bekannt. Das vorliegende Inventar konzentriert sich auf eine Überarbeitung der Tintenfisch-Ordnungen Belemnitida, Diplobelida und Vampyromorpha (Unterklasse Octobrachia), die in Ablagerungen aus der Serpentinum-Zone vorkommen, eine Abfolge, die sich im Anschluss an das Ozeanische Anoxische Event des frühesten Toarcium gebildet hat. Es wurden 111 Exemplare untersucht, und die taxonomische Analyse ergab das Vorkommen von 7 Belemnitenarten, einer Diplobelidenart und 7 Octobrachia-Arten. Die Octobrachia- und Diplobelida-Taxa kommen im unteren Teil der Serpentinum-Zone (Exaratum-Subzone) vor, während Belemniten in diesem Abschnitt selten sind und etwas häufiger im oberen Teil der Serpentinum-Zone (Falciferum-Subzone) vorkommen.

Mots clés: Systématique, paléobiodiversité, coléoidés, céphalopodes, Toarcien, schistes bitumineux, T-OAE.

Résumé

Les céphalopodes de la sous-classe Coleoidea sont des fossiles fréquents dans les schistes bitumineux du Toarcien inférieur du Luxembourg. Malgré leur présence répandue, on sait peu de choses sur leur diversité taxonomique et leur répartition stratigraphique. Le présent inventaire se concentre sur une révision des ordres de céphalopodes Belemnitida, Diplobelida et Vampyromorpha (sous-classe Octobrachia) présents dans les dépôts de la zone à Serpentinum, une succession qui s'est formée à la suite de l'événement anoxique océanique du début du Toarcien. 111 spécimens ont été examinés et l'analyse taxonomique a révélé la présence de 7 espèces de bélemnites, d'une espèce de diplobelidés et de 7 espèces d'octobrachia. Les taxons Octobrachia et Diplobelida sont présents dans la partie inférieure de la zone à Serpentinum (sous-zone à Exaratum), tandis que les bélemnites sont rares dans cet intervalle et deviennent plus fréquentes dans la partie supérieure de la zone à Serpentinum (sous-zone à Falciferum).

1 Introduction

The early Toarcian black shales of southern Luxembourg, also referred to as the Bascharage Lagerstätte (Thuy et al. 2025) have been known since almost a century for their diverse and well-preserved fossil content, encompassing mostly marine vertebrates and invertebrates but also an important percentage of terrestrial flora and fauna. A comprehensive overview on the stratigraphy and palaeobiodiversity of the "Schistes bitumineux" formation (Serpentinum Zone), as the black shales are termed by the Luxembourgish Geological Survey, has been given recently by Thuy et al. (2025). The deposits are situated on the north-eastern margin of the Paris Basin, with marine connections towards the Dorset Basin in England and the Swabian Basin in southern Germany (Hermoso et al. 2014; Thuy et al. 2025). Concerning coleoid cephalopods, they occur in large numbers but their record in the scientific literature has been scarce, except for the Octobrachia. The belemnites *sensu stricto* (order Belemnitida) occur in moderate numbers in the upper part of the "Schistes bitumineux": their number increases dramatically in the subsequent "Couches à Hildoceras bifrons" unit (Bifrons Zone, personal observation R. Weis). Lucius (1945) reported six belemnite taxa from the "Posidonienschiefer" of Luxembourg. Since then, no updated data on the belemnite diversity has been published. The diplobelids are known by one single taxon, *Chondroteuthis wunnenbergi*, previously reported from Luxembourg (Fuchs 2006). Concerning Octobrachia, the picture originating from the literature appears more consistent. Fuchs & Weis (2008, 2010) reported several taxa of loligosepiids and teudopsiids from Luxembourg. Meanwhile Fuchs et al. (2024) described *Simoniteuthis michaelyi* nov. gen. nov. sp. based on a single specimen from the Bascharage Lagerstätte. The prey-predator interactions between pachycormid fish and octobrachian coleoids on one hand (Weis et al. 2024) and ichthyosaurs and octobrachian coleoids on the other hand (Fischer et al. 2025) have also been the subject of recent studies based on material from the Luxembourgish early Toarcian. Palaeontological excavations at the Bascharage site in the early 1990ies (Godefroit 1995) and in 2022 (Thuy et al. 2025) as well as specimens collected by private fossil hunters allowed to gather a rather large number of specimens, most of which were undescribed up to date. The present catalogue represents therefore an opportunity to report a complete and taxonomically updated overview of the coleoid cephalopod fauna of the early Toarcian (Serpentinum Zone) black shales of Luxembourg, providing a unique window into coleoid diversity in the aftermath of the Toarcian Oceanic Anoxic Event in the north-eastern Paris Basin.

2 Material and methods

The studied material originates from various localities in the southern part of the Grand-duchy of Luxembourg and is stored in the public collections of the Musée national d'histoire naturelle de Luxembourg (acronym MNHNL) and the private collection of Jean-Claude Streitz (Itzig, Luxembourg). 53 belemnitid specimens have been studied, 11 diplobelid specimens, and 47 Octobrachian specimens. Among those, 7 belemnite species have been identified, one diplobelid species and 7 octobrachian species.

Terminologies and morphometric parameters follow Doyle (1990a), Weis et al. (2025) and Fuchs (2020). Synonym lists are incomplete; further synonyms can be found within the cited literature. The stratigraphic subdivision of the early Toarcian of Luxembourg follows Thuy et al. (2025).

To create the images of the belemnite specimens, we employed the "digital whitening" technique as described by Kiselev (2021), an approach more convenient than traditional chemical bleaching methods. This digital method enhances the contrast and clarity of fossil structures by processing multiple images taken from the same point of view under different lighting angles into a single composite image, without applying substances to the specimen. Initial images were captured using a Canon EOS R7 digital mirrorless camera and illuminated with a Rotolight Neo 2 LED light, allowing the repositioning of the light source between shots.

For each final image, a series of 7 to 10 photographs of a fossil were taken and subsequently combined using Adobe Photoshop. The workflow involves

importing the images as layers into a Photoshop file, followed by removing the background in each. Subsequently, one of the images is chosen as the base layer and is not processed further. All other layers are inverted into a negative state and their transparency reduced to under 10%. In the final step, the entire stack of layers is converted to grayscale and adjustments to brightness and contrast are made until the specimen features are adequately depicted, this result is then exported as a raster image file.

3 General preservation of coleoid cephalopods in the Toarcian of Luxembourg

Belemnitida/Diplobelida

Belemnite rostra are often preserved with the (crushed) phragmocone and are only found in the black shales but never in the calcareous nodules. Rostra are sometimes preserved as pyritized shells. Diplobelid remains (phragmocone, proostracum, ink sack) are preserved in shales or in flat calcareous nodules.

The 10 arms of belemnitids and diplobelids are characteristically equipped with hooks. Unfortunately, these hooks are rare in Luxembourg compared to other contemporaneous localities (e.g. Holzmaden). Also, muscular tissues of belemnitids and diplobelids are virtually unknown.

Octobrachia

Octobrachians usually preserve remains of the gladius (engl. pen; french: plume) and the muscular mantle. The originally chitinous gladius is a sturdy structure in the dorsal mantle and thus works like a "backbone" (Fig. 3). The ink owns the best preservation, but isolated ink sacs cannot be assigned. Moreover, leaked ink often smears over the gladius, which is the key character for a proper identification. The phosphatized muscular mantle is white and striated. It may help to recognize the aspect, because the dorsal gladius surface is - as a rule - free of muscular mantle (Fuchs et al. 2016). Other features such as fins, eyes, beaks, or arms are rarely preserved and represent absolute exceptions.

Gladiuses (often consisting of part and counterpart) may be embedded in dorsal, ventral or lateral aspect. Lateral specimens are difficult to determine compared to dorsoventrally embedded specimens. In fragmentary or otherwise poorly preserved specimens, it is essential to find growth increments. The course of growth increments allows to distinguish between, median field, hyperbolar zones, and lateral fields and thus to reconstruct the overall shape of the gladius (Fig. 3).

4 Systematic palaeontology

Order Belemnitida Haeckel, 1866
Suborder Belemnitina Zittel, 1895
Family Megateuthididae Sachs & Nalnjaeva, 1967

Genus *Acrocoelites* Lissajous, 1915

Acrocoelites trisulculosus (Simpson, 1855)

(Fig, 1A)

* 1855 *Belemnites trisulculosus* - Simpson, p. 26.

1984 *Acrocoelites (Toarcibelus) raui* (Werner) - Riegraf et al., p. 150, pl. 9, fig. 9.

1990 *Acrocoelites (Toarcibelus) trisulculosus* (Simpson, 1855) - Doyle, p. 37, pl. 8, fig. 4, pl. 9, figs. 1-6, pl. 10, figs. 1-3, pl. 11, figs. 1-3.

1998 *Acrocoelites (Acrocoelites) trisulculosus* (Simpson, 1855) - Schlegelmilch, p. 61, pl. 6, fig. 9.

Material - 11 specimens from the Serpentinum Zone, unspecified subzones, of Schouweiler, Bascharage, Dudelange-Bettembourg, Foetz (MNHNL TU142, TU181, TU510, TV034, TV395, TV398, Ti221, Ti230, MDB029).

Description - Large, robust, cylindriconical to cylindrical rostrum. Apex acute to very acute, bearing two well-developed dorsolateral grooves and a ventral groove which is more or less developed. Transverse sections are compressed quadrate.

Remarks - Concerning the similarities with *Acrocoelites ilminstrensis*, see below. Although the stratigraphic distribution of this species is partially overlapping with *A. trisulculosus*, the latter one occurs already in the lower part of the Serpentinum Zone.

Acrocoelites ilminstrensis (Phillips, 1867)
(Fig. 1B)

* 1867 *Belemnites ilminsterensis* - Phillips, p. 64, pl. 12, fig. 30.

1984 *Acrocoelites (Toarcibelus) ilminsterensis* (Phillips) - Riegraf et al., p 155, pl. 10.

1990 *Acrocoelites (Toarcibelus) ilminsterensis* (Phillips) - Doyle, p. 39, pl. 12, figs. 1-7.

1998 *Acrocoelites (Acrocoelites) ilminstrensis* (Phillips) - Schlegelmilch, p. 59, pl. 5, figs. 11-12.

v. 2014 *Acrocoelites ilminstrensis* (Phillips, 1867) - Pinard et al., p. 165, fig. 6C.

v. 2018 *Acrocoelites ilminstrensis* (Phillips, 1867) - Weis et al., p. 99, fig. 10G.

Material - Seven specimens from the Serpentinum Zone, Falciferum Subzone of Schouweiler, Foetz, Ehlerange (MNHNL TU277, TU996, TU997, TV386, TV396, TV418, Ti165).

Description - Medium-sized, slender cylindriconical to cylindrical rostrum. The elongate apex bears three well-developed grooves, the ventral groove is commonly longer and more deeply incised. Transverse sections depressed quadrate in the stem region, and more compressed and subquadrate in the alveolar region.

Remarks - The species bears a great similarity to *A. trisulculosus*. According to Doyle (1990), *A. ilminstrensis* can be distinguished from the former by its generally more slender, elongate rostrum and a depressed, subquadrate transverse section. Also, the stratigraphical range of both taxa differs, *A. trisulcolosus* being more common in the Exaratum Subzone and disappearing during the Falciferum Subzone, and *A. ilminstrensis* appearing in the Falciferum Subzone and persisting into the Bifrons Zone (Riegraf et al. 1984; Doyle 1990a; Schlegelmilch 1998).

Acrocoelites riegrafi Doyle, 1992
(Fig. 2D)

1984 *Acrocoelites (Acrocoelites) longiconus* (Schwegler) - Riegraf et al., p. 155, pl. 11.

1990a *Acrocoelites (Acrocoelites) longiconus* (Schwegler, 1969) - Doyle, p. 34, pl. 7, figs. 4-6, 17.

* 1992 *Acrocoelites (Acrocoelites) riegrafi* nom. nov. - Doyle, p. 75.

1998 *Acrocoelites (Acrocoelites) riegrafi* Doyle, 1992 - Schlegelmilch, p. 59, pl. 5, fig. 10.

? 2014 *Acrocoelites* cf. *riegrafi* Doyle, 1992 - Pinard et al., p. 166, fig. 6J.

Material - One specimen from the Serpentinum Zone, Falciferum Subzone of Dudelange-Bettembourg (MNHNL TV397).

Description - Medium-sized, conical to slightly subhastate rostrum with a short epirostrum in the apical part Apex acute to attenuate, commonly striated, bearing three well defined grooves. Transverse sections compressed subquadrate.

Remark - The species, previously known as *Acrocoelites longiconus* (Schwegler) (= junior subjective synonym), is a rare fossil in the Serpentinum Zone, but is rather abundant in the Bifrons Zone.

Genus *Simpsonibelus* Doyle, 1992

Simpsonibelus expansus (Simpson, 1855)
(Fig. 1C)

* 1855 *Belemnites expansus* - Simpson, p. 31.

1984 *Dactyloteuthis* (*Catateuthis*) aff. *inaudita* (Voronez) - Riegraf et al., p. 161, pl. 12, fig. 9.

1992 *Simpsonibelus expansus* (Simpson, 1855) - Doyle, p. 53, pl. 20, figs. 1-10.

2003 *Simpsonibelus expansus* (Simpson, 1855) - Doyle, p. 179, figs. 14G, H.

Material - Two specimens from the Serpentinum Zone, Falciferum Subzone of Rodange (MNHNL TV400a, b).

Description - Medium-sized, moderately robust and subcylindrical to subhastate rostrum. Apex moderately acute, bearing three apical grooves. Transverse sections subcircular to subquadrate.

Remarks - The genus *Simpsonibelus* is a rare occurrence in the upper Serpentinum Zone, becoming more frequent in the Bifrons Zone (Doyle 1992).

Genus *Cuspiteuthis* Abel, 1916 (=*Youngibelus* Riegraf, 1980)

Cuspiteuthis tubularis (Young & Bird, 1822)
(Fig. 2A)

* 1822 *Belemnites tubularis* - Young & Bird, p. 259, pl 24, fig. 6.

1984 *Youngibelus tubularis* (Young & Bird) - Riegraf et al. p 158, pl. 11, figs. 7-8.

1985 *Youngibelus tubularis* (Young & Bird, 1822) - Doyle, p. 136, pl. 1, figs. 1-5.

1992 *Youngibelus tubularis* (Young & Bird, 1822) - Doyle, p. 50, pl. 18, figs. 1-5, 7.

1998 *Youngibelus tubularis* (Young & Bird, 1822) - Schlegelmilch, p. 63, pl. 8. Figs. 7-8.

2021 *Cuspiteuthis tubularis* (Young & Bird, 1822) - Neige et al., in Synoptical taxonomic appendix S3

Material - 15 specimens from the Serpentinum Zone, unspecified subzones, of Dudelange-Bettembourg and Foetz (MNHNL TU250, TU251, TU252, TV389, TV401, Ti010).

Description - Large-sized, elongate, cylindrical rostrum with epirostrum. Apex acute, without grooves. Transverse sections elliptical to circular. No sharp boundary between ortho- and epirostrum.

Remarks - The ontogeny of this species has been fully discussed by Doyle (1985).

Cuspiteuthis trivialis (Simpson, 1855)
(Fig. 2C)

* 1855 *Belemnites trivialis* - Simpson, p. 26.

1984 *Acrocoelites laevis* (Phillips) - Riegraf et al., pl. 10, fig. 6.

1992 *Youngibelus simpsoni* (Mayer-Eymar, 1883) - Doyle, p. 51, pl. 18, fig. 6, pl. 19, figs. 1-10.

1998 *Youngibelus simpsoni* (Mayer-Eymar) - Schlegelmilch, p. 64, pl. 8, fig. 9.

2003 *Youngibelus trivialis* (Simpson, 1855) - Doyle, p. 179, figs. 13I-L.

2021 *Cuspiteuthis trivialis* (Simpson, 1855) - Neige et al., in Synoptical taxonomic appendix S3

Material - 14 specimens from the Serpentinum Zone, unspecified subzones of Dudelange-Bettembourg, Rodange and Esch/Alzette (MNHNL TU365, TU421, TV399, TV400, TV404, Ti004, Ti010, Ti236).

Description - Medium-sized, cylindrical to cylindriconical rostrum without epirostrum. Transverse sections are compressed and rounded pyriform. The apex is moderately obtuse and possesses no apical grooves, though apical striae are commonly present.

Remarks - This species is also known as *C. simpsoni* (Mayer-Eymar), a subjective junior synonym of *C. trivialis* (see Doyle 2003). This species forms a dimorphic pair with *C. tubularis*, interpreted as sexual dimorphism by Doyle (1985).

Cuspiteuthis acuaria (v. Schlotheim, 1820)
(Fig. 2B)

1848 *Belemnites acuarius gigas* - Quenstedt, p. 412, pl. 25, fig. 6.

1984 *Youngibelus gigas* (Quenstedt) - Riegraf et al., p. 158, pl. 11, figs. 9-10.

1998 *Youngibelus ohmdenensis* nom. nov. - Schlegelmilch, p. 63, pl. 8, figs. 10-11.

2000 *Cuspiteuthis acuaria* (Schlotheim, 1820) - Riegraf, p. 292, figs. 9-10, 13-14.

2014 *Cuspiteuthis acuaria* (v. Schlotheim, 1820) - Pinard et al., p. 169, fig. 8A.

2021 *Cuspiteuthis acuaria* (Schlotheim, 1820) - Neige et al., in Synoptical taxonomic appendix S3

Material - Two specimens from the Serpentinum Zone, unspecified subzone, of Dudelange-Bettembourg (MHNL TU249, Ti236).

Description - Large-sized, elongated *Cuspiteuthis*, with a sharp separation between ortho- and epirostrum. The latter is commonly crushed in the black shale facies. No apical grooves.

Remarks - Riegraf (2000) reported a continuous morphological transition from *C. tubularis* to *C. acuaria*. Attribution to either one or the other taxon is not always easily done, the main distinction being a shorter and more sharply separated orthorostrum in the latter. Furthermore, *C. acuaria* is reported to be stratigraphically younger, ranging up into the Bifrons Zone (Riegraf et al. 1984).

Order Diplobelida Jeletzky, 1965
Family Chondroteuthidae Jeletzky, 1965

Genus *Chondroteuthis* Bode, 1933

Chondroteuthis wunnenbergi Bode, 1933
(Figs. 3G, 4A)

? 1922 *Belemnoteuthis acuta*. - Naef, p. 322, fig. 64c.

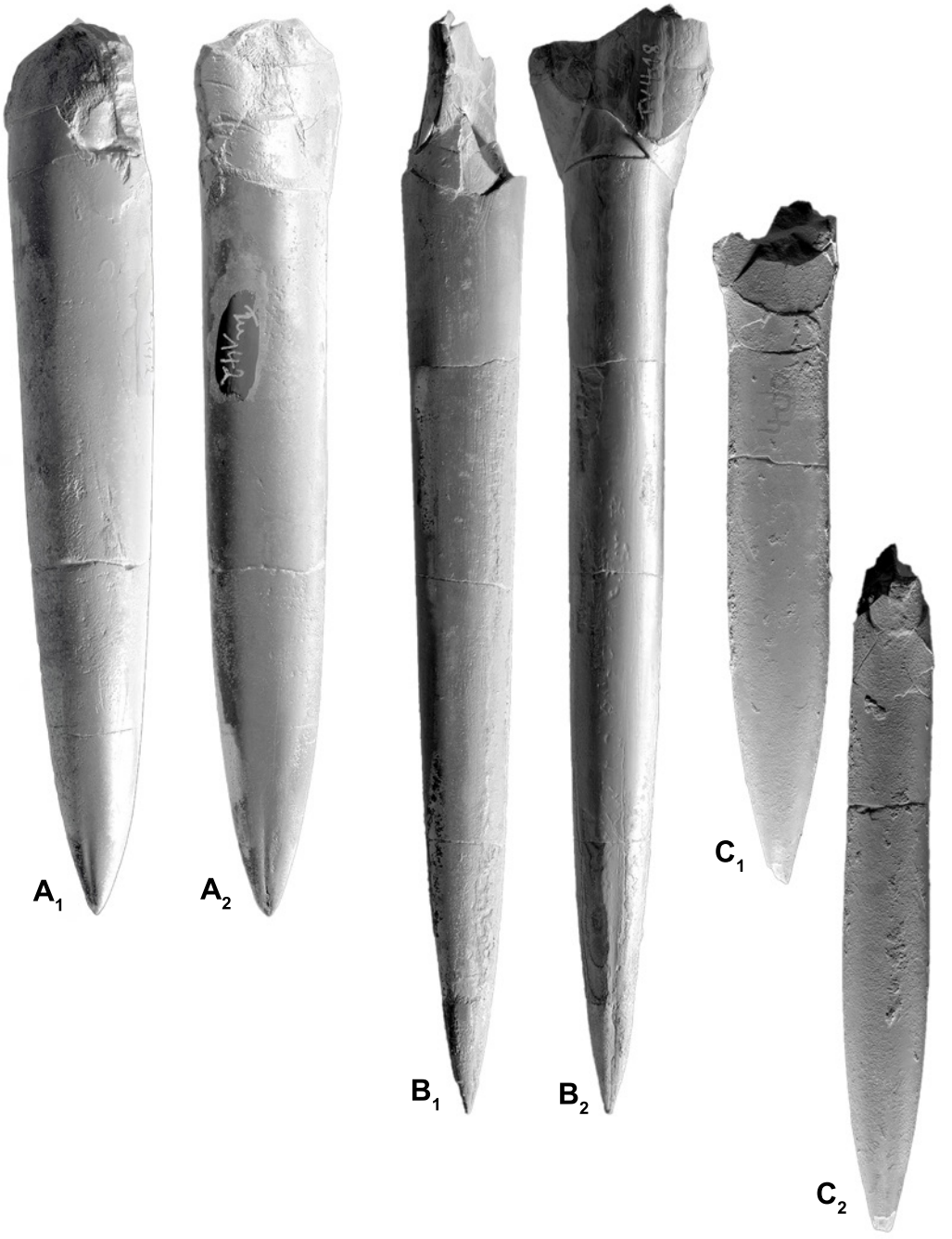


Fig. 1: Belemnites from the "Schistes bitumineux", Serpentinum Zone, Exaratum or Falciferum subzones of Luxembourg. **A** - *Acrocoelites trisulculosus* (Simpson, 1855), Schouweiler, MNHNL TU142. A_1 lateral view; A_2 ventral view. **B** - *Acrocoelites ilminstrensis* (Phillips, 1867), Sanem, MNHNL TV418; B_1 lateral view; B_2 ventral view. **C** - *Simpsonibelus expansus* (Simpson, 1855), Rodange, MNHNL TV400a. C_1 lateral view; C_2 ventral view. Size of all specimens x 1.

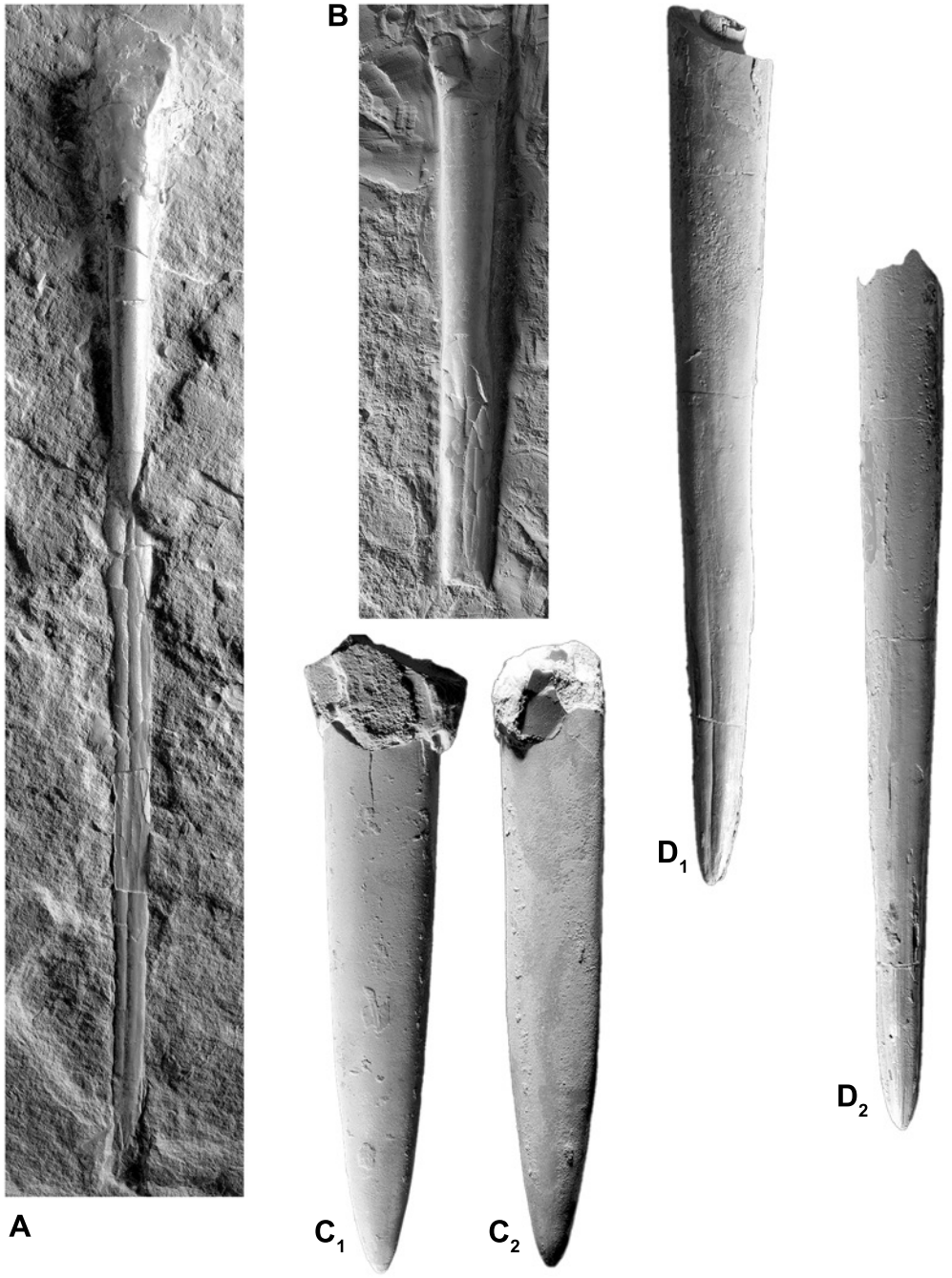


Fig. 2: Belemnites from the "Schistes bitumineux", Serpentinum Zone, Falciferum Subzone of Luxembourg. **A** - *Cuspiteuthis tubularis* (Young & Bird, 1822), Dudelange-Bettembourg, MNHNL TU250. Size x 0.5 **B** - *Cuspiteuthis acuarius* (v. Schlotheim, 1820), Dudelange-Bettembourg, MNHNL TU249. Size x 0.5. **C** - *Cuspiteuthis trivialis* (Simpson, 1855), Rodange, MNHNL TV400c. $\mathbf{C}_1$ lateral view; $\mathbf{C}_2$ ventral view. Size x1. **D** - *Acrocoelites riegrafi* Doyle, 1992, Dudelange, MNHNL TV397. $\mathbf{D}_1$ lateral view, $\mathbf{D}_2$ ventral view. Size x 1.

*v. 1933 *Chondroteuthis wunnenbergi.* Bode, p. 55, pls. 9-11.

1966 *Chondroteuthis wunnenbergi.* - Jeletzky, pl. 20, figs. 3-4.

v. 2006 *Chondroteuthis wunnenbergi.* - Fuchs, fig. 2E. (MNHL specimen)

v. 2016 *Chondroteuthis wunnenbergi.* - Hoffmann et al., figs. 2-9.

v. 2019 *Chondroteuthis wunnenbergi* Bode, 1933. - Fuchs, p. 3, figs. 4a-d.

Material - 11 specimens from the Serpentinum Zone, Exaratum Subzone of Bascharage (MNHNL TU641, TU681, TU685/699, TU760, TU764, TV272, TV815, TV967, Ti048, Ti089, Ti100)

Description - The orthoconic phragmocone opens at an angle of 15-16°. Its chambers are comparatively low (ratio chamber length-to-diameter 0.15-0.2) and the narrow pro-ostracum is anteriorly straight to weakly rounded, almost twice as long as the phragmocone. A rostrum proper is absent; only a thin sheath covers the apicalmost part of the phragmocone.

Remarks - The abundance of *Chondroteuthis wunnenbergi* in Luxembourg appears to be higher than in any other European localities. The taxon is stratigraphically limited to a single horizon, the so-called "insect nodule bed" (Fig. 3 in Thuy et al. 2025), dated from the Exaratum Subzone, which corresponds to the stratigraphic position encountered for instance in southern England (Doyle 1992). This diplobelid is known to have possessed 10 differentiated arms (ratio arm length-to-mantle length 0.45-0.5) equipped with uniserial hooks of four different types. These are still unknown from Luxembourg.

Subclass Octobrachia Haeckel, 1866
Order Vampyromorpha Robson, 1929
Suborder Loligosepiina Jeletzky, 1965

Remarks - In general, gladiuses of the Loligosepiina show strong similarities amongst the various genera and species; unambiguous determinations therefore afford well-preserved specimens. The hyperbolar zone of loligosepiids is per definition very long when compared to non-loligosepiid octobrachians (Fuchs 2020). Comparisons of the hyperbolar zone length within loligosepiids therefore afford an adjusted length classification that is not applicable e.g. for teudopseid octobrachians.

Family undetermined

Genus *Simoniteuthis* Fuchs, Weis & Thuy, 2024

Simoniteuthis michaelyi Fuchs, Weis & Thuy, 2024

(Fig. 4B)

*v. 2024 *Simoniteuthis michaelyi* nov. gen. n. sp. - Fuchs et al.: figs 2-3.

Material - One specimen (the holotype) consisting of part and counterpart, from the Serpentinum Zone, Exaratum Subzone of Bascharage (MNHNL Ti024).

Description - The extra-ordinarily well-preserved holotype exhibits the gladius surrounded by muscular mantle and the head-arm complex. The moderately wide gladius (ratio gladius $width_{max}$ to gladius length = 0.33) consists - as typical for Loligosepiina - of a median field (opening angle 11-12°), hyperbolar zones, and long lateral fields. Key character of *Simoniteuthis michaelyi* is the deeply incised V-shaped hyperbolar zone. The hyperbolar zone is long (hyperbolar zone length -to-gladius length 0.86). Its arm crown comprises eight arms.

Remarks - The gladius morphology of *Simoniteuthis michaelyi* is a mosaic of characters typical of the genera *Loligosepia* and *Parabelopeltis*.

Family Loligosepiidae Regteren Altena, 1949

Genus *Loligosepia* Quenstedt, 1839

Loligosepia aalensis (Schübler in Zieten, 1832)

(Figs. 3B, 4C)

*v. 1832 *Loligo Aalensis* Schübler - Zieten, p. 34, pl. 25, fig. 4.

1922 *Belopeltis Aalensis* (Zieten, 1830). - Naef, p. 125, fig. 47b.

1966 *Loligosepia aalensis* (Zieten, 1830). - Jeletzky, p. 33, 42, text-fig. 4D.

v. 2008 *Loligosepia aalensis* (Schübler in Zieten, 1830). - Fuchs & Weis, p. 96, figs. 2A-D, 3.

v. 2020 *Loligosepia aalensis* (Schübler in Zieten, 1830). - Fuchs, p. 14, figs. 7.1a-c.

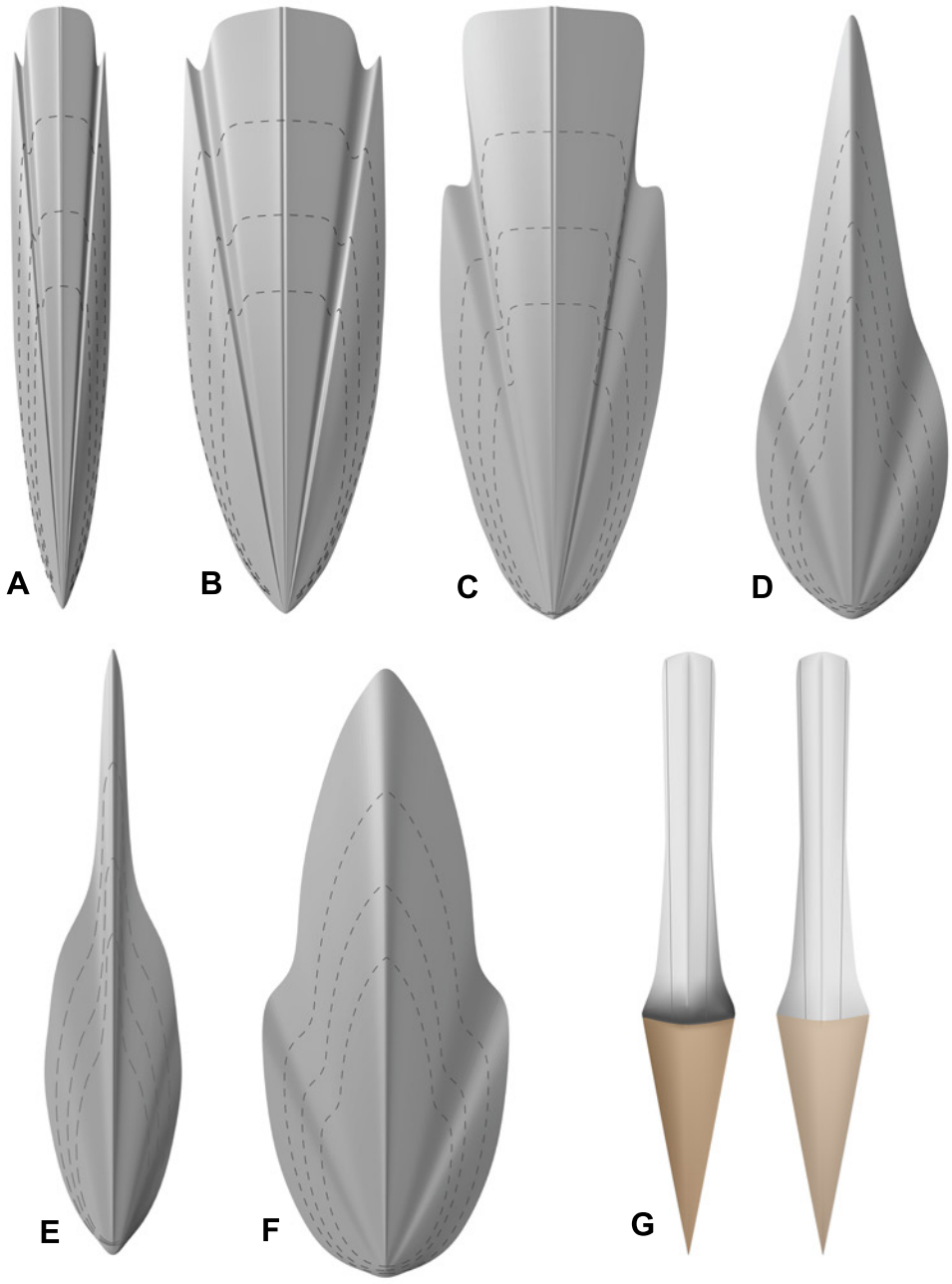


Fig. 3: Modelized 3-D gladius shape and growth increments of selected Toarcian Octobrachian and diplobelid taxa. **A** - *Jeletzkyteuthis coriaceus* (Quenstedt, 1849). **B** - *Loligosepia aalensis* (Schübler in Zieten, 1832). **C** - *Parabelopeltis flexuosa* (Münster, 1843). **D** - *Teudopsis bollensis* Voltz, 1836. **E** - *Teudopsis bunelii* Eudes-Deslongchamps, 1835. **F** - *Teudopsis subcostata* (Münster, 1843). **G** - *Chondroteuthis wunnenbergi* Bode, 1933.

Material - 11 specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg and Bascharage (MNHNL TU853a, TV109, TV197, TV244, TV277, Ti001, TV278, TU139, ?TV203, ?TV536, ?Ti155).

Description - The moderately wide gladius (ratio gladius width$_{max}$-to- median field length 0.35) is characterized by a V-shaped hyperbolar zone. The hyperbolar zone is very long (ratio hyperbolar zone length -to-gladius length 0.94). The median field opens at an angle of 15°.

Genus *Jeletzkyteuthis* Doyle, 1990

Jeletzkyteuthis coriaceus (Quenstedt, 1849)
(Figs. 3A, 5A)

1835 *Teudopsis Agassizii*, N. - Eudes-Deslongchamps, p. 72, pl. 2, fig. 15. (unclear definition)

*v 1849 *Loliginites coriaceus*. - (Quenstedt), p. 512, pl. 34, figs. 5-8.

1922 *Loliginites coriaceus* (Quenstedt, 1849). - Naef, p. 125, fig. 47c.

1990b *Jeletzkyteuthis agassizi* (Deslongchamps, 1835). - Doyle, p. 198, text-fig. 1, 3A.

1993 *Jeletzkyteuthis coriacea* (Quenstedt, 1849). - Guérin-Franiatte & Gouspy, p. 183, pl. 1, figs. 1-2.

v. 2008 *Jeletzkyteuthis coriaceus* (Schübler in Zieten, 1830). - Fuchs & Weis, p. 101, figs. 3, 5A-B.

v. 2020 *Jeletzkyteuthis coriaceus* (Quenstedt, 1849). - Fuchs, p. 15, figs. 7.2a-c.

Material - Two specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg (MNHNL TV170, TV245).

Description - The conspicuously slender gladius (ratio gladius width$_{max}$-to- median field length 0.16, opening angle of the median field 7°) is the most striking character distinguishing it from species with similar deeply incised hyperbolar zones such as *Loligosepia aalensis.* The hyperbolar zone is very long (ratio hyperbolar zone length-to-gladius length 0.94).

Remarks - Due to its overall similarity, laterally embedded gladiuses of *L. aalensis* may appear very slender and thus may be easily confused with *J. coriaceus.*

Family Geopeltidae Regteren Altena, 1949

Genus *Parabelopeltis* Naef, 1921

Parabelopeltis flexuosa (Münster, 1843)
(Fig. 3C, 5B)

*v. 1843 *Geoteuthis flexuosa*. Münster, pp. 75/6, pl. 9, fig. 2.

1922 *Parabelopeltis flexuosa* (Münster, 1843). - Naef, p. 128., fig. 47a.

1966 *Parabelopeltis flexuosa* (Münster, 1843). - Jeletzky, p. 33, text-fig. 4C.

v. 2008 *Parabelopeltis flexuosa* (Münster, 1843). - Fuchs & Weis, p. 107, figs. 3, 7A-D.

v. 2020 *Parabelopeltis flexuosa* (Münster, 1843). - Fuchs, p. 15, figs. 8.2a-b.

Material - Ten specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg and Bascharage (MNHNL TV110, TV246, TV465, coll. Streitz, TU853b, TV223, Ti154, Ti152, TU454, TV202).

Description - The moderately wide gladius (ratio gladius width$_{max}$-to- median field length 0.38) is typified by a smoothly arcuated hyperbolar zone. The hyperbolar zone length is moderate (ratio hyperbolar zone length-to-gladius length 0.82).The median field opens at an angle of 13°.

Remarks - Although already Naef (1922) pointed out the close similarities between the gladii of *Parabelopeltis flexuosa* and *Loligosepia aalensis,* misidentified specimens exist in worldwide collections. Well-preserved specimens may be delimited by hyperbolar zone length. It is significantly longer in *Loligosepia* and *Jeletzkyteuthis* than in *Parabelopeltis.* In incomplete specimens, experts focus on growth increments and their course in the hyperbolar zone.

Order Octopoda Leach, 1817
Suborder Teudopseina Starobogatov, 1983
Family Teudopseidae van Regteren Altena, 1949

Genus *Teudopsis* Eudes-Deslongchamps, 1835

Remarks - The genus *Teudopsis* is mainly restricted to the Toarcian (with a question mark in the Callovian) and contains five species. Three of them

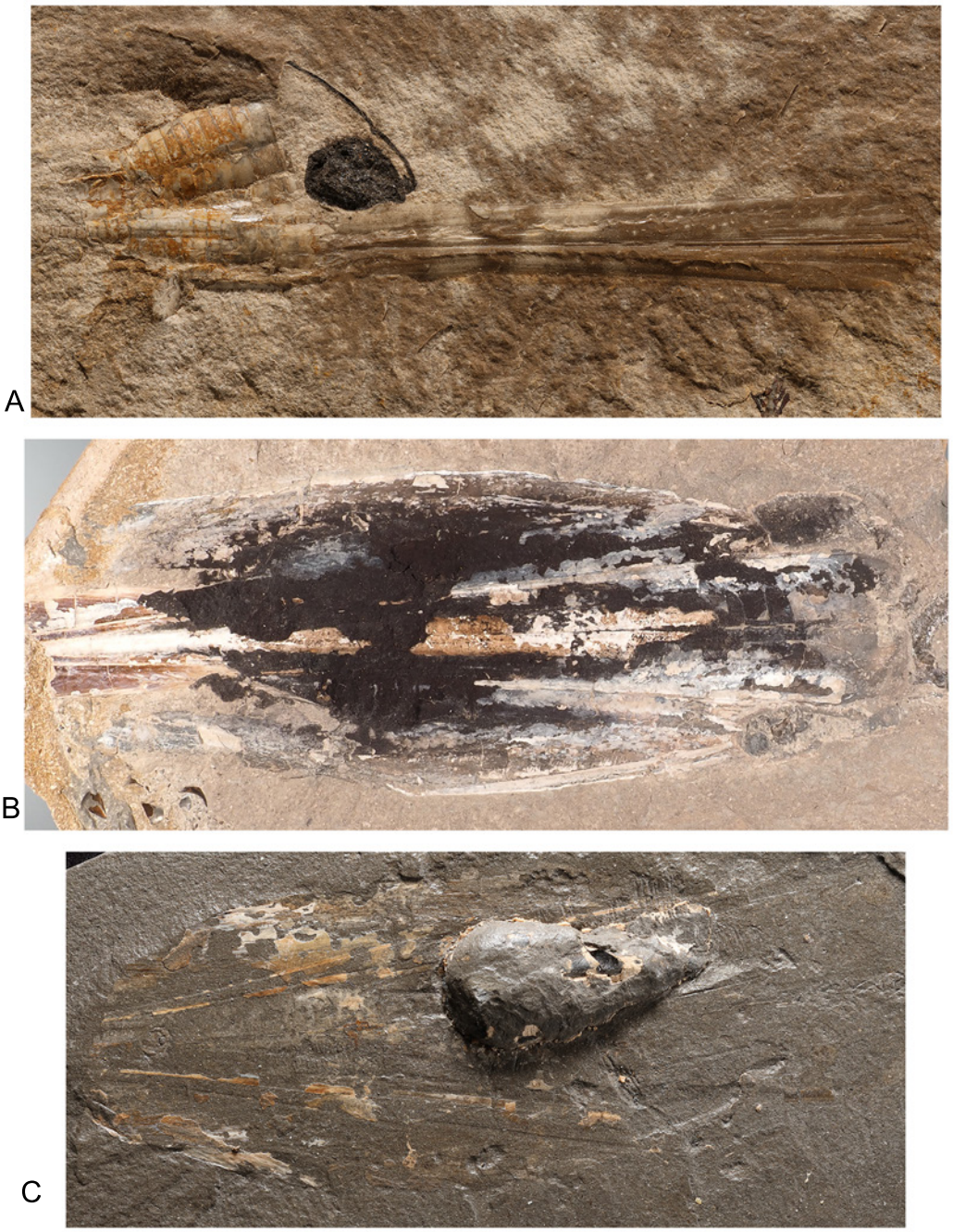


Fig. 4: Diplobelida and Octobrachia from the "Schistes bitumineux", Serpentinum Zone, Exaratum Subzone of Luxembourg. **A** - *Chondroteuthis wunnenbergi* Bode, 1933, Bascharage, MNHNL TU641. Size x 0.5. **B** - *Simoniteuthis michaelyi* Fuchs, Weis & Thuy, 2024, Bascharage, MNHNL Ti024. Size x 0.5. **C** - *Loligosepia aalensis* (Schübler in Zieten, 1832), Dudelange-Bettembourg, MNHNL TU853. Size x 1.



Fig. 5: Octobrachia from the "Schistes bitumineux", Serpentinum Zone, Exaratum Subzone of Luxembourg. A - *Jeletzkyteuthis coriaceus* (Quenstedt, 1849), Dudelange-Bettembourg, MNHNL TV245. Size x 0.5. B - *Parabelopeltis flexuosa* (Münster, 1843), Bascharage, MNHNL TV465. Size x 1.

have been recorded from Luxembourg: *T. bunelii* (type species), *T. bollensis*, and *T. subcostata*. *T. acuta* recorded in Germany and the UK is generally very rare and *T. jeletzkyi* is so far only known from South America. While the posterior gladius shape of these species is more or less indistinguishable, the relative width of the anterior part differs markedly (Fig. 3).

Teudopsis bollensis Voltz, 1836

(Figs. 3D, 6A)

*v. 1836 *Teudopsis bollensis*. Voltz, p. 149.

v 1849 *Loliginites Schübleri*. - Quenstedt, p. 499, pl. 32, fig. 15.

1922 *Beloteuthis bollensis* (Zieten, 1830). - Naef, p. 144, text-fig. 53B-d.

v. 2010 *Teudopsis bollensis* (Voltz, 1836). - Fuchs & Weis, p. 357 figs. 3, 4A-H.

v. 2020 *Teudopsis bollensis* (Voltz). - Fuchs, p. 24, figs. 14.1a-b.

Material - 15 specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg and Bascharage (MNHNL TU989, TV168,

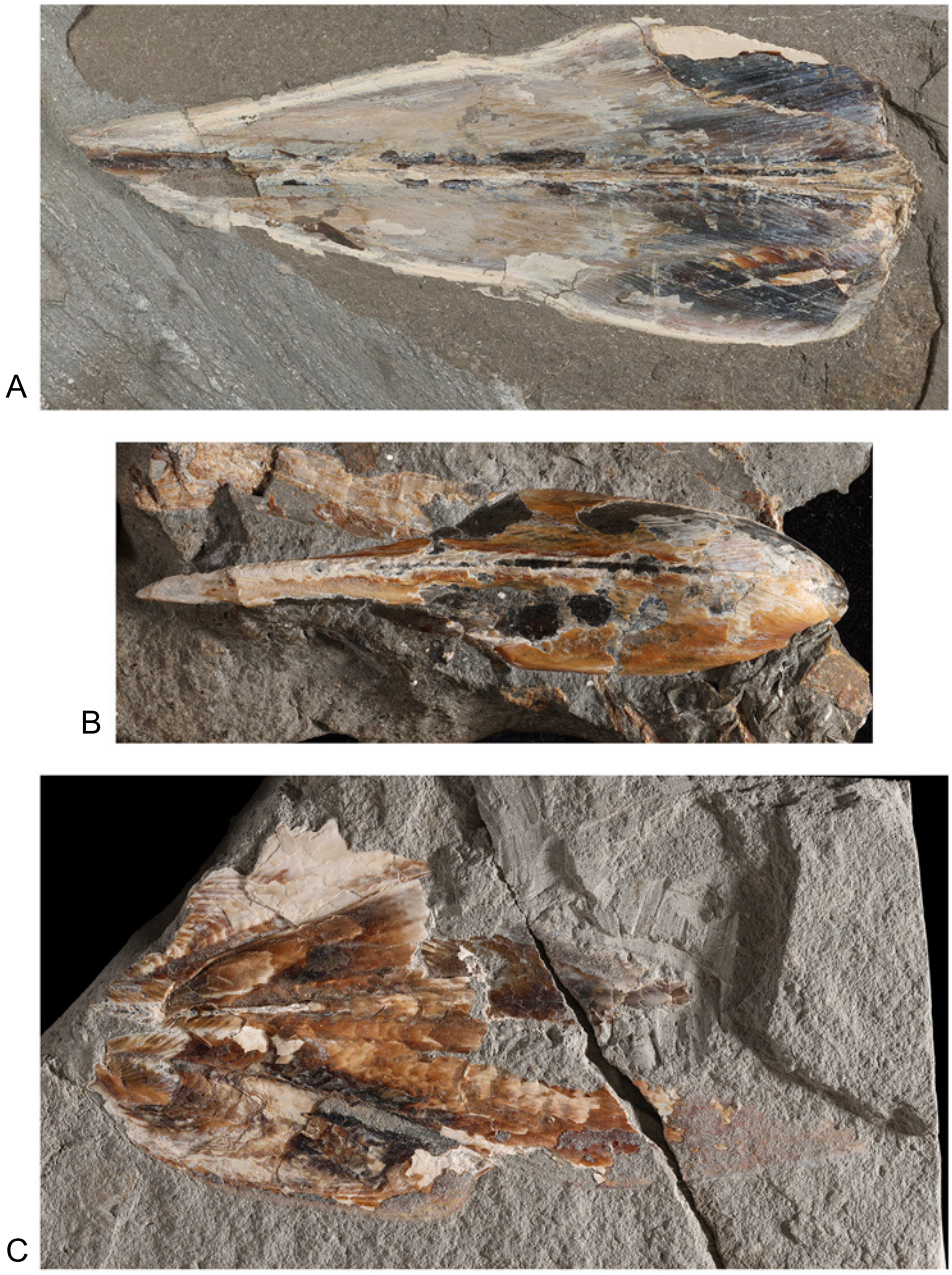


Fig. 6: Octobrachia, Teudopseidae from the "Schistes bitumineux", Serpentinum Zone, Exaratum Subzone of Luxembourg. **A** - *Teudopsis bollensis* Voltz, 1836, Bascharage, MNHNL Ti066. **B** - *Teudopsis bunelii* Eudes-Deslongchamps, 1835, Dudelange-Bettembourg, MNHNL TV234. **C** - *Teudopsis subcostata* (Münster, 1843), Bascharage, MNHNL TV248. Size of all specimens x 1.

TV236, TV228, TV288, TV535, TV598, TV952, TV953, TV956, Ti066, Ti153, Ti176, Ti196, coll. Streitz).

Description - The gladius is moderately wide (ratio gladius $width_{max}$-to- gladius length 0.34) compared to *T. bunelii* and *T. subcostata* . The anterior margins of the median field continuously converge.

Teudopsis bunelii Eudes-Deslongchamps, 1835

(Figs. 3E, 6B)

* 1835 *Teudopsis bunelii*. - Eudes-Deslongchamps, p. 74-76, pl. 3, fig. 1-3.

1922 *Beloteuthis bunellii*. Deslongchamps, 1835. - Naef, p. 145.

v. 2010 *Teudopsis bunelii* (Voltz, 1836). - Fuchs & Weis, p. 355 figs. 2A-E-3.

v. 2020 *Teudopsis buneli* (Voltz, 1836). - Fuchs, p. 24.

Material - Two specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg (MNHNL TV234, coll. Streitz).

Description - The gladius is slender (ratio gladius $width_{max}$-to- gladius length 0.23) compared to *T. bollensis*, and *T. subcostata*. The anterior margins of the median field are constricted (concave); the anterior median field therefore rachis-like.

Remarks - Since its first description, *T. bunelii* has often been confused with *T. bollensis.* In Fuchs & Weis (2010), we thoroughly corroborated the differences. The gladius of *T. bunelii* is unique in having a rachis-like anterior gladius shape (and thus resembles the gladius of Tithonian *Palaeololigo*).

Teudopsis subcostata (Münster, 1843)

(Figs. 3F, 6C)

* 1843 *Beloteuthis subcostata*. - Münster, p. 61, pl. 5, fig. 2, pl. 6, fig. 2.

1922 *Beloteuthis subcostata* Münster, 1843. - Naef, p. 142, text-fig. 53a.

1990b *Teudopsis subcostata* (Münster, 1843). - Doyle, p. 202, text-fig. 5.

v. 2010 *Teudopsis subcostata* (Münster, 1843). - Fuchs & Weis b, p. 359 figs. 5A-D.

Material - Six specimens from the Serpentinum Zone, Exaratum Subzone of Dudelange-Bettembourg, Ehlerange and Bascharage (MNHNL TU295, TU733, TU843, TV247, TV248, Ti156)

Description - *Teudopsis subcostata* owns the widest gladius (ratio gladius $width_{max}$-to- gladius length 0.43). The anterior margins of the median field are bulbous (convex).

5 Discussion

The coleoid cephalopod diversity during the early Toarcian Serpentinum Zone in southern Luxembourg is assessed herein for the first time. A few pattern that appear are worth to be highlighted and call for comparisons with coeval deposits of other European basins such as the Cleveland Basin in Yorkshire or the Swabian Basin in Southwest Germany, for which detailed data exists in the literature.

Belemnitida/Diplobelida

Although the exact stratigraphic range of the belemnites found in the "Schistes bitumineux" (Serpentinum Zone) of Luxembourg cannot always be drawn with certainty due to the analysis of older collection material that has not been collected in situ, it appears that only one taxon, *Acrocoelites trisulculosus*, is present with certainty in the lower part of the Serpentinum Zone (Exaratum Subzone). This pattern is coherent with occurrences in the Cleveland Basin (e.g. Doyle 1990a; Harries & Little 1999; Ullmann et al. 2014), where *A. trisulculosus* is the first belemnite species to be present after the biological crisis linked to the Toarcian Oceanic Anoxic Event (T-OAE) that had affected several groups of marine invertebrates including belemnites (Ullmann et al. 2014). A similar distribution has been observed in the Swabian Basin by Riegraf et al. (1984) who report only *Acrocoelites raui* (=*A. trisulculosus*) from the lower part of the Serpentinum Zone. The upper part of the Serpentinum Zone (Falciferum Subzone) records the presence of at least 6 other taxa, ascribed to the genera *Cuspiteuthis* (=*Youngibelus*), *Acrocoelites* and *Simpsonibelus*, a pattern that again is consistent with observations from the Yorkshire Basin and the Swabian Basin (Riegraf et al. 1984). Based on these observations, it can be concluded that recovery of the Belemnitida has been

progressive in the aftermath of the T-OAE, belemnites being particularly sensitive to sea-bottom anoxia (Ullmann et al. 2014).

The single taxon of Diplobelida recorded in Luxembourg, *Chondroteuthis wunnenbergi*, is limited to a single bed from the Exaratum Subzone, the so-called "nodules with insects" (Thuy et al. 2025), which has been tentatively correlated with the "Unterer Stein" bed in the Swabian Basin (Thuy et al. 2025) and has the same stratigraphic age as the *Chondroteuthis*-bearing beds in England (Fish Bed in Gloucestershire; Doyle 1992). The absolute number of *Chondroteuthis* specimens recorded from a single locality (Bascharage Lagerstätte) is remarkable compared to other localities in Germany and England. However, this could also be an effect of undersampling in the latter.

Octobrachia

The Octobrachia occur exclusively in the lower part of the Serpentinum Zone (Exaratum Subzone), at several distinct horizons (Fuchs et al. 2024; Thuy et al. 2025). The abundance of *Loligosepia aalensis* and *Jeletzkyteuthis coriaceus* is comparable to Holzmaden in the Swabian Basin (Fuchs, personal data), the comparatively high abundance of *Parabelopeltis flexuosa* in Luxembourg is an outstanding feature.

Compared to the diversity of Holzmaden, all taxa present in the well-known Posidonienschiefer Fm have also been found in Luxembourg with the notable exception of *Geopeltis simplex* and *Parabelopeltis sagittata*. It has to be noted that the latter species has been recorded elsewhere in the northeastern Paris Basin (Lorraine region, France) by Guérin-Franiatte & Gouspy (1993); hence, its absence in Luxembourg might as well just be a collection bias. On the other hand, the rare species *Simoniteuthis michaelyi*, the holotype of which originates from the Bascharage Lagerstätte in Luxembourg (Fuchs et al. 2024) has not yet been reported from England nor from Germany.

6 Acknowledgements

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Early and middle Toarcian bivalves from the Grand-Duchy of Luxembourg

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Keywords: Toarcian; Early Jurassic; bivalves; "Schistes bitumineux"; "Couches à *Hildoceras bifrons*", "Couche à *Catacoeloceras crassum*"; Grand-Duchy of Luxembourg.

Abstract

This study documents the lower and middle Toarcian bivalves from the Grand-Duchy of Luxembourg, during and in the aftermath of the Early Toarcian Oceanic Anoxic Event. The Toarcian sediments outcropping in the territory of Luxembourg were deposited on the northeastern margin of the Paris Basin. The studied material, housed in the Natural History Museum of Luxembourg, comes from the lower Toarcian "Schistes bitumineux" formation, the overlying middle Toarcian "Couches à *Hildoceras bifrons*" and the middle Toarcian "Couche à *Catacoeloceras crassum*", all of which contain low-diversity bivalve assemblages. Eleven species belonging to ten genera have been recorded, many of which have been already described and studied from other localities in previous literature. Among them, *Pseudomytiloides dubius*, *Steinmannia bronni* and *Parvamussium pumilum* are typical elements of black shales, tolerant to low-oxygen levels, as cf. *Meleagrinella* (*Praemeleagrinella*)? *golberti*.

The infaunal *Goniomya* (*Goniomya*) *rhombifera*, *Homomya* sp., *Neocrassina subtetragona* and *Palaeonucula amoena*, found higher in the stratigraphic sequence, testify the onset of recovery after the Toarcian extinction interval.

Schlüsselwörter: Toarcium; Unterjura; Muscheln; "Schistes bitumineux"; "Couches à *Hildoceras bifrons*", "Couche à *Catacoeloceras crassum*"; Großherzogtum Luxemburg.

Zusammenfassung

Diese Studie dokumentiert die Muscheln aus dem unteren und mittleren Toarcium im Großherzogtum Luxemburg während und nach dem ozeanischen Anoxieereignis im frühen Toarcium. Die Toarcium-Sedimente im heutigen Luxemburg wurden am nordöstlichen Rand des Pariser Beckens abgelagert. Das untersuchte Material, das im Naturhistorischen Museum Luxemburg aufbewahrt wird, stammt aus der unteren Toarcium-Formation "Schistes bitumineux", der darüber liegenden mittleren Toarcium-Formation "Couches à *Hildoceras bifrons*" und der mittleren Toarcium-Formation "Couche à *Catacoeloceras crassum*", die alle eine geringe Vielfalt an Muschelfunden aufweisen. Es wurden elf Arten aus zehn Gattungen erfasst, von denen viele bereits in der bisherigen Literatur von anderen Fundorten beschrieben und untersucht wurden. Unter ihnen finden sich *Pseudomytiloides dubius*, *Steinmannia bronni* und *Parvamussium pumilum*, welche typische Elemente von Schwarztonschiefer sind und wie cf. *Meleagrinella (Praemeleagrinella)*? *golberti* einen niedrigen Sauerstoffgehalt tolerieren. Die im Boden lebenden *Goniomya (Goniomya) rhombifera*, *Homomya* sp., *Neocrassina subtetragona* und *Palaeonucula amoena*, die in höheren Schichten der stratigraphischen Abfolge gefunden wurden, zeugen vom Beginn der Regeneration nach dem Toarcium-Massensterben.

Mots clés: Toarcien; Jurassique inférieur; bivalves; "Schistes bitumineux"; "Couches à *Hildoceras bifrons*", "Couche à *Catacoeloceras crassum*"; Grand-Duché de Luxembourg.

Résumé

Cette étude documente les bivalves du Toarcien inférieur et moyen du Grand-Duché de Luxembourg, pendant et après l'événement anoxique océanique du début du Toarcien. Les sédiments toarciens situés sur le territoire luxembourgeois se sont déposés sur la marge nord-est du bassin parisien. Le matériel étudié, conservé au Musée d'histoire naturelle du Luxembourg, provient des unités stratigraphiques des " Schistes bitumineux " du Toarcien inférieur, des " Couches à *Hildoceras bifrons* " du Toarcien moyen sus-jacent et de la " Couche à *Catacoeloceras crassum* " du Toarcien moyen, qui contiennent toutes des faunes de bivalves peu diversifiées. Onze espèces appartenant à dix genres ont été répertoriées,

dont beaucoup ont déjà été décrites et étudiées dans d'autres localités dans la littérature existante. Parmi elles, *Pseudomytiloides dubius*, *Steinmannia bronni* et *Parvamussium pumilum* sont des éléments typiques des argiles noires, tolérants aux faibles niveaux d'oxygène, comme cf. *Meleagrinella (Praemeleagrinella) ? golberti*. Les espèces benthiques *Goniomya (Goniomya) rhombifera*, *Homomya* sp., *Neocrassina subtetragona* et *Palaeonucula amoena*, trouvées plus haut dans la séquence stratigraphique, témoignent du début de la reprise après l'intervalle d'extinction du Toarcien.

1 Introduction

The purpose of the present study is to document the early to middle Toarcian bivalves from the Grand Duchy of Luxembourg (hereafter Luxembourg), housed in the National Museum of Natural History of Luxembourg.

The Toarcian sediments crop out in the south-west of the country, reaching a maximum thickness of nearly 160 m (Weis et al. 2024). During the Early Jurassic, this area was located in the northeastern margin of the Paris Basin, along the southern margin of the London-Brabant Massif, in a region corresponding to the Trier-Luxembourg Basin (TLB), a sub-Basin of the Paris Basin (Schintgen & Förster 2013).

The studied material comes from three lithostratigraphic units, namely: the lower Toarcian "Schistes bitumineux" formation, the overlying middle Toarcian "Couches à *Hildoceras bifrons*" and the middle Toarcian "Couche à *Catacoeloceras crassum*", which covers the upper part of the "Couches à *Hildoceras bifrons*". The former is a notable Konservat-Lagerstätte which consists of up to 60 m bituminous clay and marl ('Schistes bitumineux' in French means oil shale/bituminous shale), with a thin silty-calcareous lamination, passing towards the top into a sandier laminated marl rich in septaria; it is well constrained biostratigraphically from the Tenuicostatum Zone to the upper Serpentinum Zone (Weis et al. 2024). All the available specimens from the "Schistes bitumineux" formation come from the Exaratum Subzone of the lower Serpentinum Zone (R. Weis pers. comm.). The sediments of this unit were deposited in a relatively nearshore environment, during and in the aftermath of the Toarcian Oceanic Anoxic Event (T-OAE, ~183 Ma; Jenkyns 1988).

The middle Toarcian "Couches à *Hildoceras bifrons*" are a sequence of nodular carbonate layers ("couches" in French meaning layers) embedded in a grey-brownish marlstone (Di Cencio & Weis 2023). The carbonate nodules are a Konzentrat-type Lagerstätte, dated from the Commune Subzone of the lower Bifrons Zone (R. Weis pers. comm.).

The Middle Toarcian "Couche à *Catacoeloceras crassum*" is a brownish-rust conglomeratic and phosphatic bed, with a thickness between 0,1 and 1,5 m (Delsate & Weis 2010). In most of the Luxembourgish localities, it is a condensed bed with reworked faunas from the Bifrons and Variabilis Zones. Isotopic, sedimentological and faunistic data from this bed indicate a warming event during the middle Toarcian (boundary Bifrons-Variabilis Zones), coupled with a relatively high sea-level (Delsate & Weis 2010).

2 Material and methods

All the studied specimens are housed in the palaeontological collection of the Musée National d'Histoire Naturelle in Luxembourg (hereafter MNHNL). They have been uncovered from several localities of SW Luxembourg. The present study also includes material from unknown localities from the studied area.

3 Systematic Palaeontology

Class Bivalvia Linné, 1758
Subclass Protobranchia Pelseneer, 1889
Order Nuculida Dall, 1889
Superfamily Nuculoidea Gray, 1824
Family Nuculidae Gray, 1824

Genus *Palaeonucula* Quenstedt, 1930

Type species - *Nucula hammeri* Defrance, 1825. Original designation by Quenstedt (1930).

Palaeonucula amoena (Chapuis & Dewalque, 1853)

(Pl. 1, fig. A)

Material - One specimen, MNHNL TM497, consisting of two disarticulated valves and internal mould, Soleuvre, Middle Toarcian, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis Zones.

Description - Shell equivalve, inequilateral and well inflated, sub-trigonal in outline. Ventral margin feebly convex, anterior area longer than posterior area. Umbo inflated, placed posteriorly, sub-terminal, salient above hinge line. Beak moderately opisthogyrate. Anterior umbonal ridge moderately developed. Shell integripalliate. Anterior and posterior adductor muscle scars sub-equal, ovate. Taxodont dentition. Sculpture rather poorly preserved, consisting of commarginal growth lines.

Remarks - We ascribe the single specimen that we have at hand to *Palaeonucula amoena*, a species erected by Chapuis & Dewalque (1853) based on material from the Toarcian "marne de Grand-Cour" (Belgian Lorraine, SE Belgium), now Grandcourt Formation, the lateral equivalent of the Early Toarcian ("Schistes bitumineux" formation) to Late Toarcian (Couches à *Pseudogrammoceras fallaciosum*) deposits below the Late Toarcian to Late Aalenian Minette Ironstone Formation in Luxembourg (Taverne & Steurbaut, 2017; Weis et al., 2024 and references therein). Our specimen differs from *Palaeonucula hammeri* (Defrance, 1825), from the Lower and Middle Jurassic (Aalenian) of central Europe and Morocco, in general outline. *P. hammeri* has a sub-rectangular and more elongated shell (Tréguier, Pacaud & Prugneaux, 2017; Karapunar et al., 2020).

Species of *Palaeonucula* were probably deposit feeders, living as shallow burrowers in soft substrate (Damborenea & Pagani, 2019).

Subclass Autobranchia Grobben, 1894
Infraclass Pteriomorphia Beurlen, 1944
Order Arcida Stoliczka, 1871
Superfamily Arcoidea Lamarck, 1809
Family Parallelodontidae Dall, 1898
Subfamily Grammatodontinae Branson, 1942

Genus *Grammatodon* Meek & Hayden, 1860

Subgenus *Grammatodon* Meek & Hayden, 1860

Type species - *Arca* (*Cucullaea*) *inornata* Meek & Hayden, 1858. Original designation by Meek & Hayden (1860).

Grammatodon (*Grammatodon*) *chapuisi* (Arkell, 1930)

(Pl. 1, fig. B)

1851 *Arca elegans*; Chapuis & Dewalque 1853 (non Roemer): 178, pl. XXIV: 2a-c.

1930 *Parallelodon* (*Grammatodon*) *chapuisi*, nom. nov.; Arkell 1930: 341, not figured.

2019 *Grammatodon* (*Grammatodon*) *chapuisi* (Arkell, 1930); Knight & Morris 2019: 10, text fig. 8a-c.

2019 ?*Grammatodon* (*Grammatodon*) *chapuisi* (Arkell, 1930); Knight & Morris 2019: 10, text fig. 8d-g.

Material - Five specimens from the Middle Toarcian, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis Zones. MNHNL TM151 left valve, MNHNL TM250 articulated specimen, MNHNL TM496 articulated specimen, MNHNL TM497 articulated specimen, all from Soleuvre; MNHNL TM219 left valve, Belvaux.

Description - Strongly inflated, sub-rectangular, equivalve and inequilateral shell. Umbones inflated, broad, not sulcate, placed between one third and median. A well-defined, sharp umbonal carina runs from umbones to posteroventral end. Ornamentation of left valve coarser than that of right valve. Strong radial sculpture is present on both valves; in the left valve it gives rise to a shallow cancellate pattern where radial ribs cross the commarginal sculpture. In the right valves that we have at hand, radial ribs are pronounced on the anterior and, especially, the posterior area, while the rest of the shell is almost smooth, with hardly discernible radial sculpture, best seen on the umbonal area. Hinge plate dentition not observable.

Remarks - Chapuis & Dewalque (1853) assigned a form characteristic of the Toarcian marne de Grand-Cour (Grandcourt Fm.) to *Arca elegans* (Römer, 1836); the latter one, however, as already pointed out by Arkell (1930) and later by Knight & Morris (2019), is a different species: indeed, among others, Römer's *elegans* is characterized by a distinct sulcus. Therefore, Arkell (1930) proposed the name *chapuisi* for Chapuis & Dewalque's *elegans*.

Grammatodon was interpreted as epibyssate, semi-infaunal or infaunal by authors (see discussion and references in Ros-Franch et al., 2014). Knight & Morris (2019) pointed out that sediment associations of the studied British Lower Jurassic *Grammatodon* (*Grammatodon*) material, suggests there are 'sediment to form' correlations.

The Lower Jurassic *Grammatodon (Grammatodon) inaequivalvis* (Goldfuss, 1837) features a shell sculpture characterized by a different ornament between the left and right valves, that of the left one being coarser, as in *G.* (*G.*) *chapuisi*. Etter (2010) suggested an epibenthic, reclining mode of life on soft bottoms for the former, which was resting on its left valve on and partially submerged in the sediment, with the reticulate ornament of the left valve helping in anchoring the shell in the substrate. The same mode of life was suggested by Knight & Morris (2019) for *G.* (*G.*) *chapuisi*, as well as for *Grammatodon* (*Grammatodon*) *interruptus* (Moore, 1866).

Order Myalinida Paul, 1939
Superfamily Inoceramoidea Giebel, 1852
Family Inoceramidae Giebel, 1852

Genus *Pseudomytiloides* Cox, 1969 (ex Koshelkina, 1963)

Type species - *Mytiloides marchaensis* Petrova, 1947. Subsequent designation by Cox (1969).

Pseudomytiloides dubius (J. de C. Sowerby, 1829)

(Pl. 1, fig. C)

1829 *Inoceramus dubius* sp. nov.; J. de C. Sowerby 1829: 162, pl. 584: 3.

2009 '*Parainoceramus*'*dubius* (J. de C. Sowerby, 1828); Knight & Morris 2009: 974, pl. 5: 11-16.

2015 *Parainoceramya*? *dubia* (Sowerby, 1829); Ros-Franch et al. 2015: 21, pl. 1: 6.

2023 *Pseudomytiloides dubius* (Sowerby, 1828); Little et al. 2023: 137, text figs 2, 3A-D.

Material - All specimens come from the Lower Toarcian "Schistes bitumineux" formation (Exaratum Subzone, Serpentinum Zone). MNHNL TU116, MNHNL TU180, MNHNL TU196, MNHNL TU218, MNHNL TU238, MNHNL TU250, MNHNL TU303, MNHNL TU304, MNHNL TU380, MNHNL TU421, MNHNL TU468, MNHNL TU603, MNHNL TU852, MNHNL TU933, MNHNL TV119, MNHNL TV159, MNHNL TV164, MNHNL TV179, MNHNL TV245, MNHNL TV259, MNHNL TV310, Bettembourg-Dudelange; MNHNL TU513, Bettembourg; MNHNL TU242, MNHNL TU249, MNHNL TV099, MNHNL TV123, MNHNL TV160, MNHNL TV331, Dudelange; MNHNL TU160, Schouweiler; MNHNL TU177, MNHNL TU628, MNHNL TU630, MNHNL TU652, MNHNL TU653, MNHNL TU654, MNHNL TU660, MNHNL TU669, MNHNL TU676, MNHNL TU682, MNHNL TU683, MNHNL TU719, MNHNL TU743, MNHNL TU783, MNHNL TU791, MNHNL TU792, MNHNL TU888, MNHNL Ti162, Bascharage; MNHNL TU212, MNHNL TU624, MNHNL TU889, MNHNL TU901, MNHNL TU902, MNHNL TV034, MNHNL TV468, MNHNL TV543, MNHNL TV601 Foetz; MNHNL TU342, Noertzange; MNHNL TU410, Esch-Lallange; MNHNL TU417, MNHNL TU478, MNHNL TU479, MNHNL TU484, MNHNL TV384, Mondercange; MNHNL TU528, MNHNL TU799, MNHNL TV556, Sanem; MNHNL TU251, MNHNL TU365, MNHNL TU383, MNHNL TU458, MNHNL TU525, MNHNL TU991, MNHNL TU992, MNHNL TV158, unknown localities.

Description - Shell equivalve, inflated, suboval in outline, obliquely elongated. Umbones inflated, slightly protruding above straight hinge margin. Beaks subterminal, prosogyrate. Anterior margin slightly concave, posterior margin convex, ventral margin broadly rounded. Shell thin, ornamented with irregularly spaced commarginal plicae and regular growth lamellae.

Remarks - The studied material is mostly preserved as compressed shells (both composite, inner and external moulds), but uncompacted shells and, rarely, free articulated specimens are present as well. Some specimens are coated with a thin layer of pyrite. *P. dubius* sometimes form dense pavements. Within the studied material, specimens are usually associated with ammonites, but also coleoidea and vertebrate remains such as fishes, ichthyosaurs and plesiosaurs, as well as wood and plant fragments.

Little et al. (2023) argue that, while a pseudoplankton interpretation of *P. dubius* is consistent with observation of specimens attached on wood from the lower Toarcian Posidonia Shale in Germany, the Mulgrave Shale of the Cleveland Basin in Yorkshire and the Strawberry Bank Lager-

stätte in Somerset (UK), the presence of specimens not associated with wood or other potentially floating substrates in the fish bed concretions from the latter, seems to confirm the facultative pseudoplanktonic mode of life for this species.

In modern oxygen minimum zones, the mytiloid *Amygdalum anoxicolum* Oliver, 2001, tolerant to depleted oxygen conditions, provides a likely extant analogue for *P. dubius* (Danise et al., 2013).

Order Ostreida Férussac, 1822
Superfamily Ostreoidea Rafinesque, 1815
Family Gryphaeidae Vialov, 1936

Genus *Liostrea* Douvillé, 1904

Type species - *Ostrea hisingeri* Nilsson, 1832. Subsequent designation by Hudson & Palmer (1976).

Liostrea sp.
(Pl. 1, fig. D)

Material - All specimens come from the Lower Toarcian "Schistes bitumineux" formation (Exaratum Subzone, Serpentinum Zone). MNHNL TU762, MNHNL TU775, MNHNL TU652, MNHNL TU653, MNHNL TU654, encrusted ammonites, Bascharage.

Description - Inequilateral and inequivalve shell, crescentic to irregular in outline. Hinge area and internal area not visible on the studied material. Shell margin not plicate; absence of a radial posterior sulcus. Sculpture is of irregular commarginal growth lamellae.

Remarks - The available specimens show overgrowth on ammonite conchs. Oysters have been repeatedly reported in the literature to settle on ammonoids syn-vivo or post mortem (Seilacher, 1982a; Etter, 1996; Schmidt-Röhl & Röhl, 2003; Zell, Beckmann & Stinnesbeck, 2014; Kosenko & Seltser, 2016; Hautmann, Ware & Bucher, 2017 and references therein).

Examination of material from the Posidonienschiefer Formation of SW Germany by Seilacher (1982a) and Schmidt-Röhl & Röhl (2003) gave evidence of colonization when the ammonites were still alive or the shells were drifting in the water column, that is a pseudonektonic mode of life. Indeed, oysters are found on both flanks. Zell et al. (2014) suggested that bivalve settlement on nektonic hosts occurs as an ecological response to oxygen-depleted bottom environment.

Superfamily Posidonioidea Neumayr, 1891
Family Posidoniidae Neumayr, 1891

Genus *Steinmannia* Fischer, 1886

Type species - *Posidonia Bronnii* Goldfuss, 1835. Original designation by Fischer (1886).

Steinmannia bronni (Voltz in Zieten, 1833)
(Pl. 1, fig. E)

1833 *Posidonia bronnii* Voltz in Zieten 1833: 72, pl. LIV: 4.

1835 *Posidonia Bronnii* nobis; Goldfuss 1835: 119, pl. CXIII: 7a-e, ?pl. CXIV: 1.

1835 *Posidonia radiata* nobis; Goldfuss 1835: 119, pl. CXIV: 2.

1853 *Posidonomya Bronni*; Chapuis & Dewalque 1853: 208, pl. XXX: 6.

1965 '*Posidonia*' *radiata* Goldfuss; Jefferies & Minton 1965: 179, pl. 19: 5.

2009 *Bositra radiata* (Goldfuss, 1836); Caswell, Coe & Cohen 2009 suppl. mat: text fig. 5.

Material - All specimens come from the Lower Toarcian "Schistes bitumineux" formation (Exaratum Subzone, Serpentinum Zone). MNHNL TU149, Noertzange; MNHNL TU338, Schouweiler; MNHNL TU367, MNHNL TV315, unknown localities; MNHNL TU532, MNHNL TU887-1 foto, Bettembourg-Dudelange; MNHNL TV559, Dudelange; MNHNL TU849, Foetz; MNHNL TV324, Sanem.

Description - Shell equivalve, subequilateral, sub-orbicular to oval. Umbones submedian, moderately inflated, slightly salient above dorsal margin. Small, pointed beak. Dorsal margin straight to obtusely angulated; anterior, posterior and ventral margins evenly convex. Posterior end with shallow groove, running obliquely from beak to posterior margin. Hinge not observable in the studied material. Ornament is of strong, regular commarginal ridges, that become densely packed toward the ventral margin.

Remarks - The available specimens occur as isolated valves or articulated shells with the

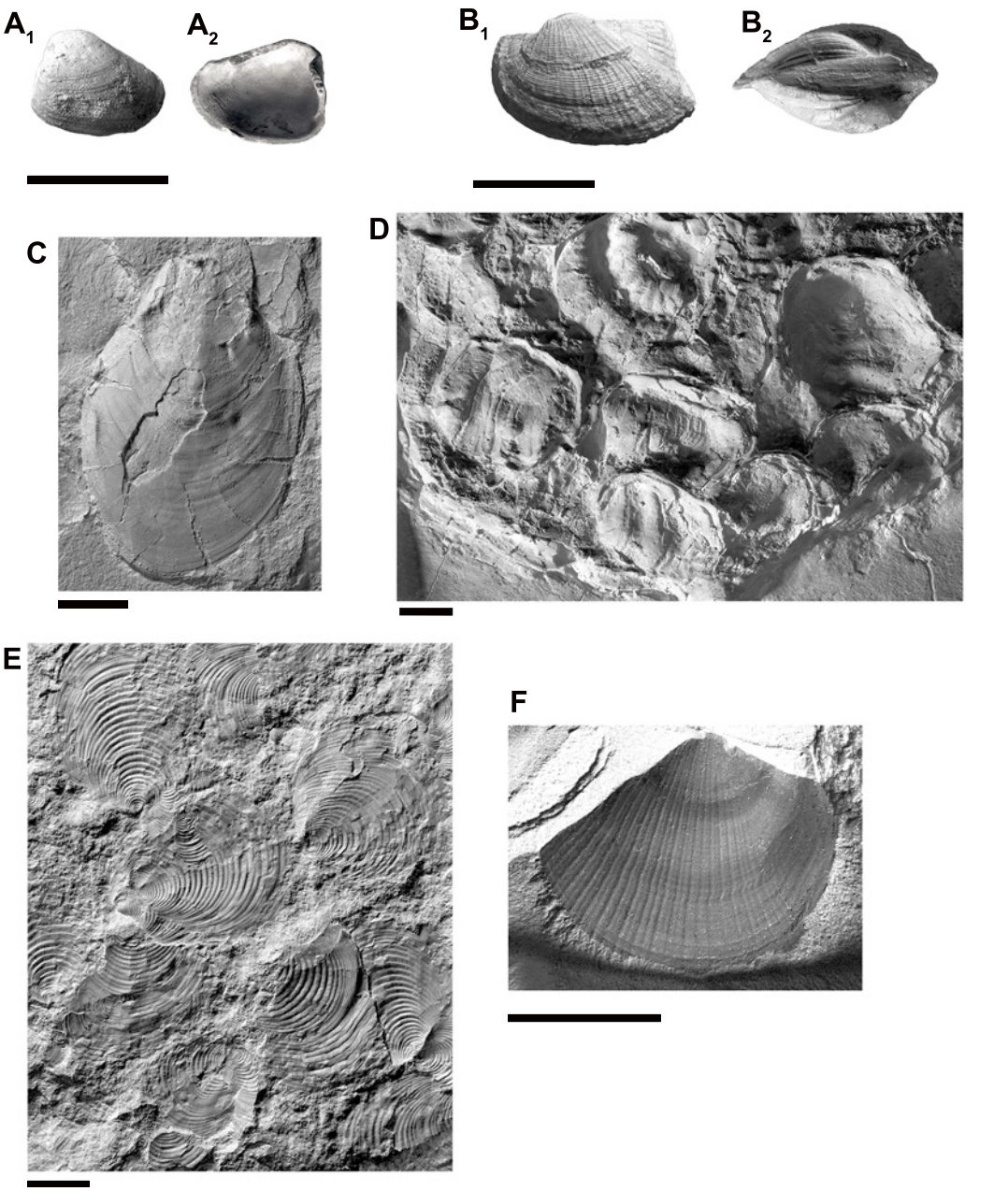


Plate 1: **A** - *Palaeonucula amoena* (Chapuis & Dewalque, 1853), n° MNHNL TM497, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis zones, Soleuvre. A_1 right valve, A_2 internal view of right valve. **B** - *Grammatodon* (*Grammatodon*) *chapuisi* (Arkell, 1930), n° MNHNL TM496, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis zones, Soleuvre, articulated specimen. B_1 left valve view, B_2 dorsal view. **C** - *Pseudomytiloides dubius* (J.de C. Sowerby, 1829), n° MNHNL Ti162, "Schistes bitumineux", Serpentinum Zone, Bascharage, left valve. **D** - *Liostrea* sp., n° MNHNL TU762, "Schistes bitumineux", Serpentinum Zone, Bascharage, several specimens encrusted on ammonite. **E.** - *Steinmannia bronni* (Voltz in Zieten, 1833), n° MNHNL TV559, "Schistes bitumineux", Serpentinum Zone, Dudelange, several specimens. **F** - cf. *Meleagrinella* (*Praemeleagrinella*)? *golberti* Lutikov & Arp, 2023, n° MNHNL TU528, "Schistes bitumineux", Serpentinum Zone, Sanem, left valve. - All scale bars: 1 cm.

valves spread wide open (butterfly preservation) and sometimes form dense pavements. Although *Steinmannia* Fischer, 1886 exhibits external resemblance with *Bositra* de Gregorio, 1886, it shows however multiple ligament pits (i.e. a multivincular ligament), whilst *Bositra* has an alivincular ligament. Indeed, Guillaume (1927) found multiple ligament pits on the ligament areas of specimens of *S. bronni* from a nodule within the "Couches à *Hildoceras bifrons*" from the surroundings of Nancy (French Lorraine, E France).

Steinmannia had most likely the same mode of life of *Bositra*. The latter was variously interpreted as free swimmer, pseudoplanktonic, nektoplanktonic or benthic (see Ros-Franch et al., 2014 and references therein); Etter (1996) provided evidence that it was benthic, a non byssate reclined mode of life would have been the most likely according to Waller in Waller & Stanley (2005).

Order Pectinida Gray, 1854
Superfamily Oxytomoidea Ichikawa, 1958
Family Oxytomidae Ichikawa, 1958

Genus *Meleagrinella* Whitfield, 1885

Subgenus *Praemeleagrinella* Lutikov & Shurygin, 2010

Type species - *Meleagrinella subolifex* Polubotko, 1968. Original designation by Lutikov & Shurygin (2010).

cf. *Meleagrinella* (*Praemeleagrinella*)? *golberti* Lutikov & Arp, 2023

(Pl. 1, fig. F)

cf. 2023a *Meleagrinella* (*Praemeleagrinella* (?)) *golberti* sp. nov.; Lutikov & Arp 2023: S57, pl I: 1-12. (and references therein)

Material - One specimen, MNHNL TU528, Sanem, Early Toarcian, "Schistes bitumineux" (Exaratum Subzone, Serpentinum Zone).

Description - Incomplete left valve, low and inequilateral, partly embedded in matrix. The posterior wing is wide. The ornament consists of irregular radial ribs of two orders along the valve. The posterior of the valve apparently lacks radial ribbing.

Remarks - We tentatively ascribe a single, incomplete specimen to *M.* (*P.*)? *golberti* because of the shape of the outer margin of posterior wing; indeed, *M.* (*P.*)? *golberti* has a bow-shaped posterior wing as seen in our specimen. The studied material is found in association with *P. dubius*. *M.* (*P.*)? *golberti* is the earliest representative of the genus *Meleagrinella* in the Toarcian (Lutikov, 2024).

M. (*P.*)? *golberti* could lead a pseudoplanktonic lifestyle, attaching to floating algae or shells of living ammonites, with the possibility of active movement as an adaptation to depleted oxygen conditions in the Early Toarcian seas (Lutikov & Arp, 2023a).

Subgenus *Clathrolima* (Cossman, 1908)

Type species - *Meleagrinella* (*Clathrolima*) *lamenti* (Cossmann, 1908). Original designation by Cossmann (1908).

Meleagrinella (*Clathrolima*) *substriata* (Münster, 1831)

(Pl. 2, fig. A)

1831 *Monotis substriatus* sp. nov.; Münster 1831: 406.

1835 *Monotis substriata* Münster; Goldfuss 1835: 138, pl. CXX: 7a-f.

1853 *Avicula substriata*; Chapuis & Dewalque 1853: 206, pl. XXVI: 5.

2024 *Meleagrinella* (*Clathrolima*) *substriata* (Münster, 1831); Lutikov 2024: 900, pl. XI: 1-10. (cum syn.)

Material - All the specimens come from the Middle Toarcian, "Couches à *Hildoceras bifrons*" (Commune Subzone, lower Bifrons Zone). MNHNL TU 101, MNHNL TU134, MNHNL TU140, MNHNL TU141, MNHNL TU386, MNHNL TU398, MNHNL TU403, MNHNL TU405, MNHNL TU408, MNHNL TU409, MNHNL TU435, MNHNL TU448, MNHNL TU450, MNHNL TU522, MNHNL TV510, MNHNL TV521, MNHNL TV594, Sanem; MNHNL TU126, MNHNL TU319 LV, MNHNL TU411, MNHNL TU418, Niederkorn; MNHNL TU333, Bascharage; MNHNL TU349, Esch-/Alzette; MNHNL TU452, MNHNL TV023, Belvaux; MNHNL TU453, Bettembourg?; MNHNL TV076, Bettembourg; MNHNL TU455, MNHNL TV056, MNHNL TV318, unknown localities; MNHNL TU649, Foetz; MNHNL TU878,

Dudelange; MNHNL TV 020, MNHNL TV025, MNHNL TV090, MNHNL TM469, Soleuvre.

Description - Shell inequilateral. Left valve subquadrate in outline, slightly higher than long, prosocline, inflated. Umbo of left valve moderately inflated, sub-median. Posterior auricle obtuse-angled. Posterior margin of the left valve with a S-like curvature.

Ornament is of dense, irregular fine radial riblets separated by broader inter-rib spaces with secondary riblets.

Remarks - The specimens that we have at hand are disarticulated left valves rather poorly preserved, forming mass accumulations in carbonate nodules.

According to Lutikov (2024), *M.* (*C.*) *substriata* settled as colonies and were attached with byssus to algae and driftwood. Following Schmidt-Röhl and Röhl (2003) study of overgrowth on ammonite conchs of the Lower Toarcian Posidonia Shale, the same author pointed out that *M.* (*C.*) *substriata* could form "benthic islands" by attaching to hard parts of the shells of other dead organisms, including ammonites.

Superfamily Pectinoidea Rafinesque, 1815

Family Propeamussiidae Abbott, 1954

Genus *Parvamussium* Sacco, 1897

Type species - *Pecten* (*Pleuronectes*) *duodecimlamellatus* Bronn, 1831. Original designation by Sacco (1897).

Parvamussium pumilum (Lamarck, 1819)

(Pl. 2, fig. B)

1819 *Pecten pumilus* sp. nov.; Lamarck 1819: 183.

1853 *Pecten personatus*; Chapuis & Dewalque 1853: 216, pl. XXVIII: 4.

1874 *Pecten pumilus* (Lamarck); Dumortier 1874: 195, pl. XLIV: 1-5.

1984 *Propeamussium* (*Propeamussium*) *pumilum* Lamarck, 1819: Johnson 1984: 23, pl. I: 1-4, 7-9. (cum syn.)

2015 *Parvamussium pumilus*; Dick 2015: 357, text fig. 3D.

Material - One specimen, MNHNL TU112, internal mould, Lower Toarcian, Bettembourg-Dudelange, "Schistes bitumineux" formation (Exaratum Subzone, Serpentinum Zone).

Description - Internal mould of a small equilateral shell of nearly 5 mm of length. Disc suborbicular, with straight anterior and posterior margins and convex ventral margin. Dorsal region missing. Ornament is of ten radial costellae terminating nearly at 5/6 of shell total height.

Remarks - The specimen is preserved on an ichtyosaur rostrum. A single specimen of *Parvamussium pumilum* has been recorded to date in Luxembourg, whereas it is very abundant at certain horizons in the Posidonienschiefer of SW Germany, notably at Göppingen, where it forms a shell bed (Johnson, 1984), and at certain levels in the Toarcian of the Causses (France) (Fürsich et al., 2001).

Today, scallops within the Propeamussiidae family inhabit the oceanic bathyal and abyssal zones, with species recorded from 200 m to more than 5,000 m (Ros-Franch et al., 2014; Kamenev, 2018 and references therein), but during the Jurassic *Parvamussium* had a neritic (<200 m depth) distribution (Damborenea, 2002a). As stated by Waller (2006), many extant propeamussiids are free living recliners on deep-water fine-grained sediments, but others are associated with coarser sediment and at least juveniles have a byssate stage (Johnson, 1984; Damborenea, 2002a and references therein). Living species, at least, of *Parvamussium* can probably swim for short distances (Ros-Franch et al., 2014 and references therein).

P. pumilum was possibly epibenthic and unattached for most of its life and able to live on a wide variety of substrates under variable environmental conditions (Johnson, 1984 and references therein).

Infraclass Heteroconchia Gray, 1854
Subterclass Archiheterodonta Giribet in Taylor et al., 2007
Order Carditida Dall, 1889
Superfamily Crassatelloidea Férussac, 1822
Family Astartidae d'Orbigny, 1844

Subfamily Astartinae d'Orbigny, 1844

Genus *Neocrassina* Fischer, 1886

Type species - *Astarte obliqua* Deshayes, 1830. Subsequent designation by Dall (1903).

Neocrassina subtetragona (Münster in Goldfuss, 1841)

(Pl. 2, fig. C)

1836 *Astarte subtetragona* Münster; Roemer, 113. (nomen dubium)

1841 *Astarte subtetragona*; Münster in Goldfuss 1841: 190, 304, pl. 134: 6.

1853 *Astarte subtetragona*; Chapuis & Dewalque 1853: 150, pl. XXII: 4.

1874 *Astarte subtetragona* (Munster); Dumortier 1874: 176, pl. XL: 5-6.

Material - All specimens come from the Middle Toarcian, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis Zones. MNHNL TM151, MNHNL TM251 left valve, TM490 (one specimen, disarticulated valves and internal mould), TM491 (one specimen, disarticulated valves and internal mould), TM492 (disarticulated valves of a single specimen), TM493 (two left valves), TM494 (two left valves and a right valve of different specimens), TM495 (left and right valves of different specimens), TM499 (two left valves and a right valve of different specimens), TM500 (one specimen, disarticulated valves and internal mould), all from Soleuvre; MNHNL TM219, several specimens, Belvaux.

Description - Shell sub-quadrangular in outline, equivalved and inequilateral; inflation low. Umbone placed at the anterior third. Postero-umbonal ridge absent. Beak small, pointed, prosogyrate. Interior of valves features a hinge plate with robust dentition, comprising two laterals and two cardinals in each valve. Musculature dimyarian. Pallial line simple, integripalliate. Internal ventral margin crenulate: ridges subrounded in the available material. Ornament is of regular commarginal ribs and dense growth lines, converging toward the anterior end.

Remarks - This species was first described by Roemer (1836: 113) who did not figure it and, later, by Goldfuss (1841). For a historical overview, see Karapunar et al. (2020). According to Knight, Collins & Morris (2024), many *Astarte subtetragona* specimens from UK museum collections are actually *Neocrassina lurida* (J. Sowerby, 1816), as likely is *A. subtetragona* figured by Chapuis & Dewalque (1853). Karapunar et al. (2020) tentatively ascribe *A. subtetragona* to *Neocrassina gueuxii* (d'Orbigny, 1850), adding that it might be a successor of *N. gueuxii*.

As stated by Knight, Collins & Morris (2024), *Neocrassina* representatives are found in a variety of facies, but most species are known from fine-grained sediments deposited in shallow, tectonically controlled basins and possibly lived in unstable (high energy) environments, but their form was not controlled by substrate type. *Neocrassina* is a shallow infaunal suspension feeder (Ros Franch et al., 2014).

Subterclass Euheterodonta Giribet & Distel, 2003
Superorder Anomalodesmata Dall, 1889
Superfamily Pholadomyoidea King, 1844
Family Pholadomyidae King, 1844

Genus *Goniomya* Agassiz, 1842

Subgenus *Goniomya* Agassiz, 1842

Type species - *Mya angulifera* J. Sowerby, 1819. Subsequent designation by Herrmannsen (1847).

Goniomya (*Goniomya*) *rhombifera* (Goldfuss, 1841)

(Pl. 2, fig. D)

1841 *Lysianassa rhombifera* sp. nov.; Goldfuss 1841: 264, pl. 154: 11.

2009 *Goniomya rhombifera* (Goldfuss, 1844); Caswell, Coe and Cohen 2009: 866, text fig. 5e; suppl. mat: text figs. 7-9.

2019 *Goniomya* (*Goniomya*) *rhombifera* (Goldfuss, 1840); Hodges 2019: 122: pl. 12: 16, pl. 13: 1, 2; text figs. 129, 130. (cum syn.)

2022 *Goniomya rhombifera*; Ferrante, Menkveld-Gfeller & Cavin 2022: 15, text fig. 2C, F.

Material - One specimen, MNHNL TM522 left valve, Sanem, Middle Toarcian, "Couches à *Hildoceras bifrons*", Lusitanicum Horizon of the lower Bifrons Zone.

Description - Left valve of an inequilateral elongated shell, moderately inflated. Umbone feebly inflated, placed nearly at one third of length. Beak acute and prosogyrate. The ornament consists of commarginal truncated v-shaped ribs, separated

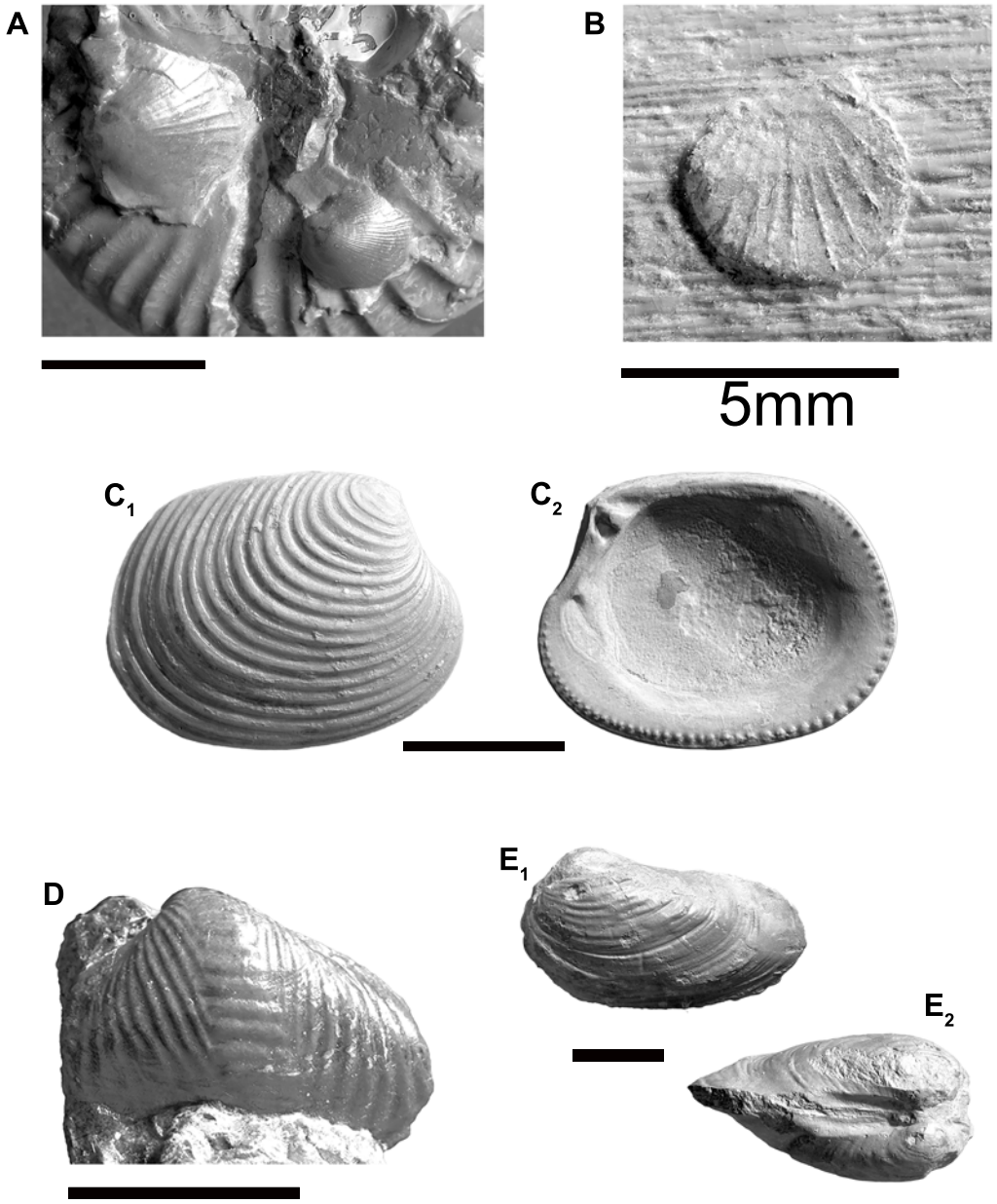


Plate 2: **A** - *Meleagrinella* (*Clathrolima*) *substriata* (Münster, 1831), n° MNHNL TM469, "Couches à *Hildoceras bifrons*", Bifrons Zone, Soleuvre, two left valves on ammonite shell. **B** - *Parvamussium pumilum* (Lamarck, 1819), n° MNHNL TU112, "Schistes bitumineux", Serpentinum Zone, Bettembourg-Dudelange, ?right valve internal mould attached on ichthyosaur bone. **C** - *Neocrassina subtetragona* (Münster in Goldfuss, 1841), n° MNHNL TM491, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis zones, Soleuvre. **C_1** internal view of right valve, **C_2** right valve. **D** - *Goniomya* (*Goniomya*) *rhombifera* (Goldfuss, 1841), n° MNHNL TM522, "Couches à *Hildoceras bifrons*", Bifrons Zone, Sanem, left valve. **E** - *Homomya* sp., n° MNHNL TM489, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis zones, Soleuvre, articulated specimen. **E_1** left valve view, **E_2** dorsal view. - Scale bars A, C-E: 1 cm; scale bar B: 5 mm.

by larger horizontal ribs in the middle of the valve that run from umbo to the ventral margin.

Remarks - As reported by Caswell, Coe & Cohen (2009), in the Cleveland Basin (Yorkshire, UK), *G.* (*G.*) *rhombifera* is abundant at the level of the Top Jet (now Mulgrave Shale Member, Whitby Mudstone Formation).

*Goniomy*a, like most members of the family Pholadomyidae, was a deep infaunal suspension feeder (Ros-Franch et al., 2014).

Genus *Homomya* Agassiz, 1842

Type species - *Mactra gibbosa* J. Sowerby, 1813. Subsequent designation by Herrmannsen (1847).

Homomya sp.

(Pl. 2, fig. E)

Material - One specimen, MNHNL TM489, Middle Toarcian, "Couche à *Catacoeloceras crassum*", condensed Bifrons/Variabilis Zones, Soleuvre.

Description - Shell inequilateral, equivalve, posteriorly elongate, moderately inflated, tapering towards posterior. Umbones moderately inflated, salient, placed anteriorly nearly at one fourth of shell length from the anterior end; beaks slightly prosogyrate, elevated above hinge. Umbonal posterior carina fading towards posteroventral margin; another ridge marks the outline of a narrow and moderately deep escutcheon. Slight posterior gape present. Commarginal sculpture is of irregular growth rugae and striae throughout the whole shell; radial ornamentation absent. Neither radial ornament nor pustules are discernable on the available specimen.

Remarks - The available specimen is damaged. It is here assigned to *Homomya* on the ground of moderately inflated valves, narrow and deep escutcheon, and absence of radial sculpture and pustule. *Homomya* most probably was a deep infaunal suspension feeder (Ros Franch et al., 2014).

4 Concluding remarks

This study adds to our knowledge of the Early and Middle Toarcian bivalve faunas from NW Europe and the extent of biotic recover from the early Toarcian mass extinction, by inclusion of data from Luxembourg.

Eleven species belonging to ten genera are described here. One genus is assigned to the Subclass Protobranchia (*Palaeonucula*), seven are assigned to the Subclass Autobranchia, Infraclass Pteriomorphia (*Grammatodon* (*Grammatodon*), *Pseudomytiloides*, *Liostrea*, *Steinmannia*, cf. *Meleagrinella* (*Praemeleagrinella*)?, *Meleagrinella* (*Clathrolima*), *Parvamussium*), one to the Infraclass Heteroconchia, Subterclass Archiheterodonta (*Neocrassina*), two to the Subterclass Euheterodonta (*Goniomya* (*Goniomya*) and *Homomya*).

Many of the taxa reported here belong to a faunal stock characteristic of several localities of the European shelf sea, and have been already described in previous literature (e.g. Goldfuss, 1833-1841; Chapuis & Dewalque, 1853; Caswell, Coe & Cohen, 2009).

As a whole, the identified bivalve assemblages are of low diversity, and distinct both regarding the taxonomic composition and the featured palaeoecological groups. Epibenthic, possibly free recliners and facultative pseudoplanktonic bivalves dominate the "Schistes bitumineux". The "Couches à *Hildoceras bifrons*" records the first appeareance of infaunal elements after the T-OAE. The following "Couche à *Catacoeloceras crassum*" comprises both shallow and deep burrowers, shallow infaunal deposit feeders, as well as a possible free recliner.

The bivalve assemblage from the Lower Toarcian "Schistes bitumineux" is of low diversity and high abundance, being dominated by *Steinmannia bronni* and *Pseudomytiloides dubius*, which sometimes form dense pavements. *Liostrea* sp. and a single specimen of *Parvamussium pumilum* and cf. *Meleagrinella* (*Praemeleagrinella*)? *golberti* have been uncovered from the same unit as well. *S. bronni*, *P. dubius* and *P. pumilum* are well-known low-oxygen specialists of black shales. *P. dubius* most probably was a facultative pseudoplanktonic, like *M.* (*P.*)? *golberti*. *P. pumilum* and *S. bronni* were most likely epibenthic.

The following nodular carbonate layers of the "Couches à *Hildoceras bifrons*" of the Middle Toarcian Commune Subzone of the lower Bifrons Zone, are characterized by a thanatocoenosis with mass accumulations of *Meleagrinella* (*Clathrolima*) *substriata* and record a single specimen of the deep burrowing suspension feeder *Goniomya* (*Goniomya*) *rhombifera*. The nodules contain also mass accumulations of the shallow infaunal brachiopod *Lingularia longoviciensis* Terquem, 1855. Lingulides are adapted to inhabit stressed environments and have been regarded as "disaster taxa" that can occupy vacant niches in the aftermath of extinction events (Paz et al., 2023 and references therein).

Higher in the Toarcian sequence, in the conglomeratic bed "Couche à *Catacoeloceras crassum*" at the top of the "Couches à *Hildoceras bifrons*", bivalves are still of low abundance and taxonomic diversity, but feature increasing palaeoecological diversity: the studied assemblage counts the possibly free-lying, reclined *Grammatodon* (*Grammatodon*) *chapuisi*, deep and shallow infaunal bivalves (respectively *Homomya* sp. and *Neocrassina subtetragona*), together with the infaunal deposit feeder *Palaeonucula amoena*.

As a whole, our study is in agreement with benthic macrofaunal palaeocommunities in epicontinental seas of NW Europe of very similar composition during the T-OAE, being dominated by 2-3 bivalve species only, adapted to deoxygenation, throughout the Serpentinum Zone in the Cleveland Basin (UK), Paris Basin and SW German Basin (Caswell & Dawn, 2019 and references therein), followed by slow recovery progression starting in the Middle Toarcian Commune Subzone of the Bifrons Zone, with the appeareance of infaunal bivalves. As pointed out by Caswell & Dawn (2019), an impoverished benthos persisted across NW Europe, and as conditions improved (Commune and Fibulatum subzones), benthic communities became dominated by species with affinities for organic rich substrates, and a greater diversity of life and feeding habits.

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Preliminary report on the palaeoflora from Toarcian marine sediments in Luxembourg

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Keywords: Jurassic, *Otozamites*, *Ptilophyllum*, *Pagiophyllum*, Toarcian, *Widdringtonites*.

Abstract

This study presents fossil plants from the Toarcian stage (Early Jurassic), curated in the palaeobotanical collection of the National Museum of Natural History in Luxembourg (MNHNL). Most fossil specimens originate from the lower Toarcian, while only a few are from the upper Toarcian. The research indicates that the plant assemblage is dominated by Coniferales and Bennettitales (Cycadeoideales), whereas tree ferns (Osmundales) and horsetails (Equisetopsida) are less frequently represented. Ginkgoales and seed ferns (Pteridospermales) are each represented by a single specimen. In total, 23 taxa were identified, of which 10 belong to conifers and 6 to bennettites. These groups were likely the dominant components of the zonal vegetation. The upper and dominant forest canopy was formed by conifers, while the lower forest layers were composed of Bennettitales and tree ferns. The ecological position of Pteridospermales and Ginkgoales remains unclear.

Schlüsselwörter: Jurazeit, *Otozamites*, *Ptilophyllum*, *Pagiophyllum*, Toarcian, *Widdringtonites*.

Zusammenfassung

Diese Studie befasst sich mit fossilen Pflanzen aus dem Toarcium (früher Jura), die in der paläobotanischen Sammlung des Nationalmuseums für Naturgeschichte in Luxemburg (MNHNL) aufbewahrt werden. Die meisten fossilen Exemplare stammen aus dem unterem Toarcium, während einige wenige aus dem oberen Toarcium stammen. Die Forschungsergebnisse zeigen, dass die Pflanzengesellschaft von Coniferales und Bennettitales (Cycadeoideales) dominiert wird, während Baumfarne (Osmundales) und Schachtelhalme (Equisetopsida) weniger häufig vertreten sind. Ginkgoales und Samenfarne (Pteridospermales) sind jeweils mit einem einzigen Exemplar vertreten. Insgesamt wurden 23 Taxa identifiziert, von denen 10 zu den Koniferen und 6 zu den Bennettiten gehören. Diese Gruppen waren wahrscheinlich die dominierenden Bestandteile der Vegetation in dieser Zone. Der obere und dominante Waldbestand wurde von Koniferen gebildet, während die unteren Waldschichten aus Bennettitales und Baumfarnen bestanden. Die ökologische Position von Pteridospermales und Ginkgoales bleibt ungeklärt.

Mots clés: Jurassique, *Otozamites*, *Ptilophyllum*, *Pagiophyllum*, Toarcien, *Widdringtonites*.

Résumé

Cette étude présente des plantes fossiles du Toarcien (Jurassique inférieur) conservées dans la collection paléobotanique du Musée national d'histoire naturelle du Luxembourg (MNHNL). La plupart des spécimens fossiles proviennent du Toarcien inférieur, tandis que seuls quelques-uns datent du Toarcien supérieur. Les recherches indiquent que l'assemblage végétal est dominé par les Coniferales et les Bennettitales (Cycadeoideales), tandis que les fougères arborescentes (Osmundales) et les prêles (Equisetopsida) sont moins fréquentes. Les Ginkgoales et les fougères à graines (Pteridospermales) sont représentées chacune par un seul spécimen. Au total, 23 taxons ont été identifiés, dont 10 appartiennent aux conifères et 6 aux bennettites. Ces groupes constituaient probablement les composants dominants de la végétation zonale. La canopée supérieure et dominante était formée de conifères, tandis que les couches forestières inférieures étaient composées de Bennettitales et de fougères arborescentes. La position écologique des Pteridospermales et des Ginkgoales reste incertaine.

1 Introduction

The National Museum of Natural History in Luxembourg (MNHNL) houses an interesting but yet undescribed palaeofloral collection originating from Toarcian marine sediments. The plant material was collected from several sites in southern Luxembourg. Most fossils belong to the lower Toarcian (approximately 70 specimens), while only five were recovered from upper Toarcian layers. Due to this disparity in specimen numbers, the present study focuses on a detailed analysis of the lower Toarcian vegetation, whereas the upper Toarcian material is treated only taxonomically.

2 Materials and methods

The analysis was conducted on 70 plant fossil specimens from the lower Toarcian, collected in southwestern Luxembourg. The specimens are housed in the National Museum of Natural History of Luxembourg (MNHNL).

Some of the fossil material consists of plant detritus that could not be identified and is therefore recorded simply as "plant material". The fossils are generally well preserved as compressions and impressions of leaves, twigs, and trunks, though cuticles are mostly absent. A few specimens are preserved as pith casts or permineralised trunks.

Identification was based on macromorphological and anatomical characteristics of leaves, pinnules, and trunks, including overall leaf or pinnule shape, attachment of pinnules to the rachis, leaf arrangement on twigs, venation type and pattern, as well as comparisons with nearest living relatives (NLR).

Palaeoecological reconstruction and forest canopy interpretation were based on comparisons with autochthonous recent forest associations of predominantly subtropical to tropical type. Since *Magnoliopsida* (flowering plants) did not yet exist during the Toarcian, special attention was given to extant relict communities in which tree ferns, cycads, and conifers co-occur —primarily in Australia, New Zealand, and Japan (Lucas & Dawson 2003; Coral & Pryer 2013; Noben et al. 2017; Abe et al. 2021, as well as personal observations).

Whenever more than one specimen of a given taxon was found, the number of specimens is indicated in parentheses following the taxon name.

The following literature was used in the process of identification and classification of plant fossils: Barbacka et al. 2014; Diéguez et al. 2009; Gee 2010; Jarzynka 2016; Konijnenburg-van Cittert 2008; McIver 2001; Pott et al. 2008; Stewart & Rothwell 1993; Thomas & Batten 2001; Wang et al. 2008; Wilde 2001.

3 Palaeoflora of the lower Toarcian

Amongst the fossils of plants from the lower Toarcian (Falciferum and Bifrons ammonite zones) that were found in the southwestern part of Luxembourg, there are representatives of tree ferns, horsetails, seed ferns, ginkgo, bennettites and conifers.

Class. Equisetopsida - horsetails

Ordo: Equisetales

Fossil material: compression, impression and casts

Equisetites sp.
Equisetum sp.
Neocalamites elegantulus Maubeuge
Neocalamites sp. (3x)

Class. Polypodiopsida - ferns

Ordo Osmundales

Fam. Osmundaceae

Fossil material: pinna compression

Cladophlebis minor Saporta (2x)

Class: Gymnospermopsida

Ordo: Pteridospermales seed ferns

Fam. Caytonaceae

Fossil material: compression and impression of a single leaflet

Sagenopteris phillipsii Brong.

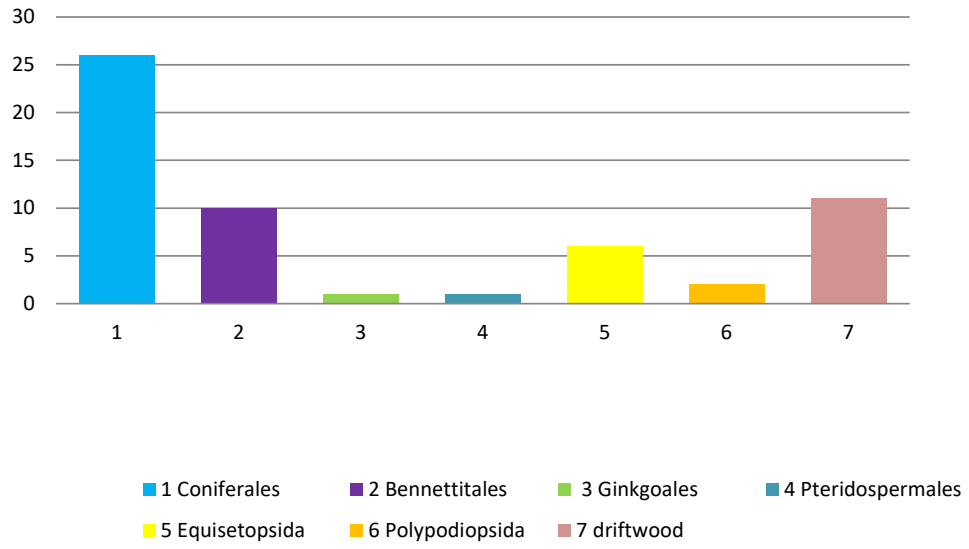


Fig. 1: Representation of higher taxa by number of fossils.

Ordo: Ginkgoales

Fam. Ginkgoaceae

Fossil material: impressions of one quite damaged leaf

Ginkgoites sp.

Ordo: Bennettitales syn. Cycadeoideales

Fam. Williamsoniaceae

Fossil material: compressions and impressions of leaves

Otozamites cf. *thomasii* Harris (2x)
Otozamites reglei (Brong.) Saporta (2x)

Pterophyllum subaequale (Hartz) Harris (2x)

Ptilophyllum pecten Phillips
Ptilophyllum sp. (2x)

Zamites sp.

Ordo: Coniferales - conifers

Fossil material: compressions and impressions of leafy twigs

Fam. Cupressaceae

Widdringtonites liasinus Kurr.
Widdringtonites reichii Ett. (7x)
? *Widdringtonites* sp.
Cupressaceae cf. *Widdringtonites* (strobilus)
Cupressaceae cf. *Widdringtonites* (megastrobilus)

Fam. Araucariaceae

Brachyphyllum sp.
Dadoxylon sp. syn. *Agathoxylon* sp.
Pagiophyllum kurri (Schimper) Salfeld (5x)
Pagiophyllum cf. *kurri* (Schimper) Salfeld
Pagiophyllum sp.

Coniferales indet.

Coniferales aff. *Frenelopsis* sp.
Coniferales gen. et sp. indet. (4x)

Gen. et sp. indet.

driftwood (12x), probably Coniferales detritus indet. (16x)

Coniferales: Most of the compressions and impressions represent apical portions of leafy twigs. Additionally, one fertilized ovulate cone (*strobilus*) and one unfertilized ovulate cone (*megastrobilus*)

were recovered.The most abundant morphogenera are *Widdringtonites* (Pl. 1, figs A-B) and *Pagiophyllum* (Pl. 1, figs. C-E), together comprising approximately 30% of the fossil material. One specimen of *Brachyphyllum* was also recovered, as well as a specimen resembling the Cretaceous genus *Frenelopsis*.

The assemblage also contained numerous pieces of driftwood, most likely originating from conifers. One specimen was identified as *Dadoxylon* sp., while the others remain unidentified. All specimens, regardless of their taxonomic placement, display pronounced xeromorphic features—small, pointed, and densely arranged leaves—which are, in fact, characteristic of conifers in general.

Bennettitales (Cycadeoideales) are represented by at least 15% of the specimens. The morphogenera *Otozamites* (Pl. 2, figs, A-B), *Ptilophyllum* (Pl. 2, fig. C), and *Pterophyllum* (Pl. 3, fig. A) dominate, comprising several species. One specimen of *Zamites* (Pl. 3, fig. B) was also identified. Compressions and impressions of entire small leaves or their fragments were found, but no large leaves or their parts were preserved. The leaves of bennettites are generally large and heavy, which likely hindered their transport to the depositional environment. Therefore, it is very likely that *Bennettitales* made up more than 15% of the original vegetation, but most of their leaves did not reach the site of deposition.

Pteridospermales: Only one leaflet of the genus *Sagenopteris* (Pl. 3, fig. C) was found. *Sagenopteris* has compound leaves with four leaflets (Thomas & Batten, 2001), which abscise individually. This means that a single *Sagenopteris* leaf has several times more potential to become fossilized than, for example, a simple *Ginkgo* leaf. Since only one seed fern leaflet was found in the examined material, we may reasonably conclude that seed ferns were very rare in the lower Toarcian flora of Luxembourg and likely represented relict elements.

Ginkgoales: This group of plants is represented by only one identifiable but rather poorly preserved specimen of *Ginkgoites* (Pl. 4, fig. A), which cannot be determined to species level. The current stage of analysis does not provide a satisfactory explanation for the poor representation of the ginkgo group in the lower Toarcian flora of Luxembourg.

Equisetales: Pith casts of *Neocalamites* (Pl. 4, fig. B) have been found, along with impressions of stems or twigs bearing leaves (*Neocalamites*, *Equisetites*, and *Equisetum*). Pith casts, which are characteristic of *in situ* fossilization, indicate that horsetails grew in close proximity to the depositional environment and thus had a greater chance of being fossilized than other taxa. This is consistent with their ecological role as representatives of azonal swamp vegetation. The percentage of *Equisetales* in the fossil assemblage is approximately 5%, although their actual proportion in the original zonal vegetation was likely much lower.

Polypodiopsida are represented by only two specimens of the tree fern *Cladophlebis minor* (Pl. 4, fig. C). The low abundance of tree ferns, which typically inhabit humid and warm environments, is probably accurate and reflects their actual presence in the original vegetation. The near absence of tree ferns may suggest that air and soil humidity in this plant community was not sufficiently high to support the development of larger populations.

4 Zonal palaeovegetation reconstruction of the studied lower Toarcian flora

Although the examined material originates from several different localities within Luxembourg, it is still taxonomically homogeneous, with the same genera being common across most of the sites. Based on this, we can conclude that the fossil material represents zonal vegetation. The fact that plant fossils were found in marine sediments—often together with marine fauna—indicates that this vegetation occupied coastal areas adjacent to the ocean.

Based on the analysis of the fossil material, it can be concluded that the vegetation represents a subtropical-Mediterranean-type forest, dominated by gymnosperms—primarily conifers and bennettites.

Conifers such as *Widdringtonites* and *Pagiophyllum* formed the upper canopy layer and were likely exposed to xerothermic conditions (intense sunlight, wind), as suggested by their xeromorphic features, which are similar to those of present-day

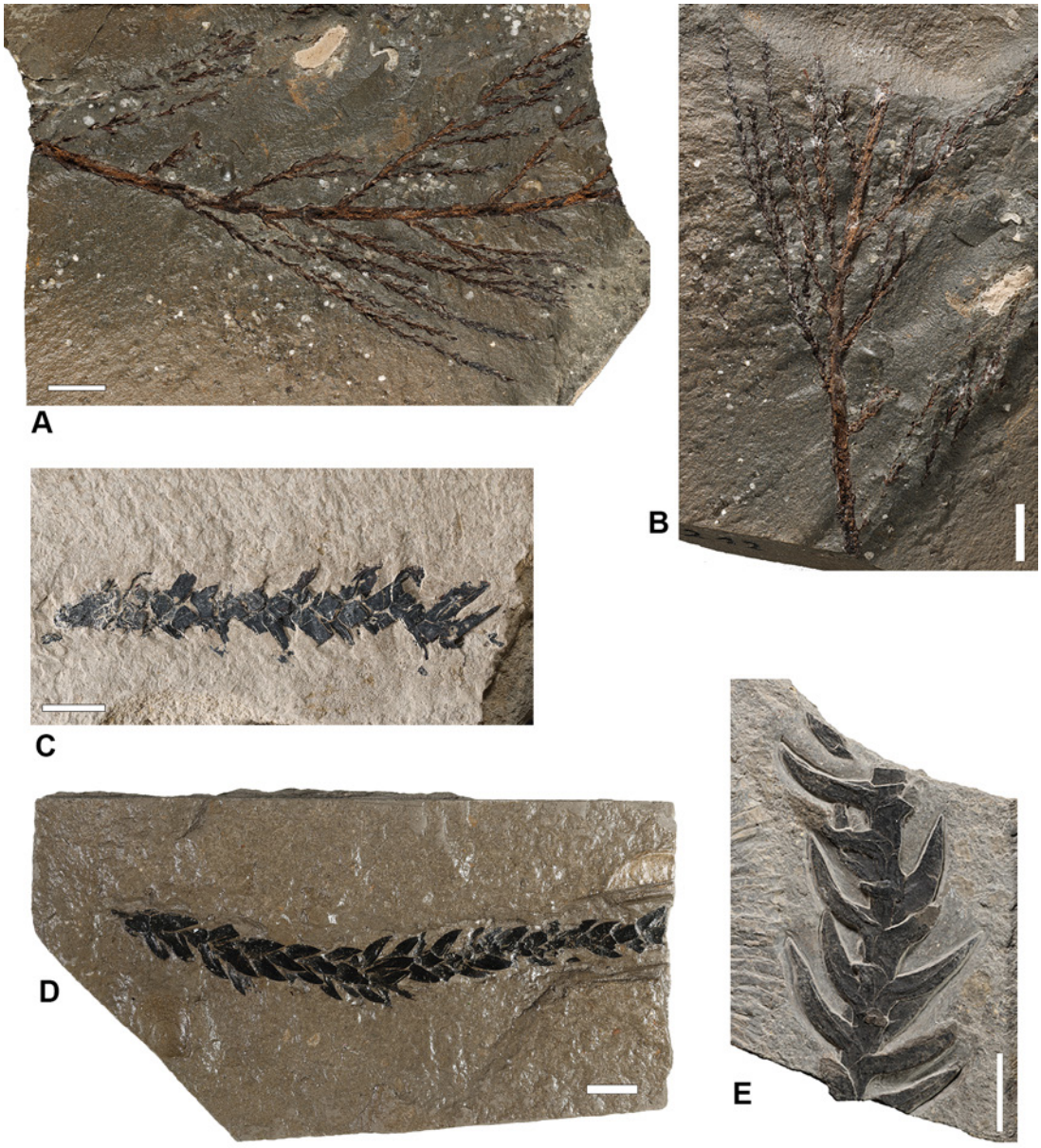


Plate 1: A - *Widdringtonites reichii* Ett., MNHNL TU219, Dudelange, Serpentinum Zone, lower Toarcian. **B** - *Widdringtonites reichii* Ett., MNHNL TV336, southwestern Luxembourg, Serpentinum Zone, lower Toarcian. **C** - *Pagiophyllum kurri* (Schimper) Salfeld, MNHNL TU305, Dudelange, Serpentinum Zone, lower Toarcian. **D** - *Pagiophyllum kurri* (Schimper) Salfeld, MNHNL TV069, southwestern Luxembourg, Serpentinum Zone, lower Toarcian. **E** - *Pagiophyllum kurri* (Schimper) Salfeld, MNHNL TV388, Foetz, Serpentinum Zone, lower Toarcian. Scale bar: 1 cm.

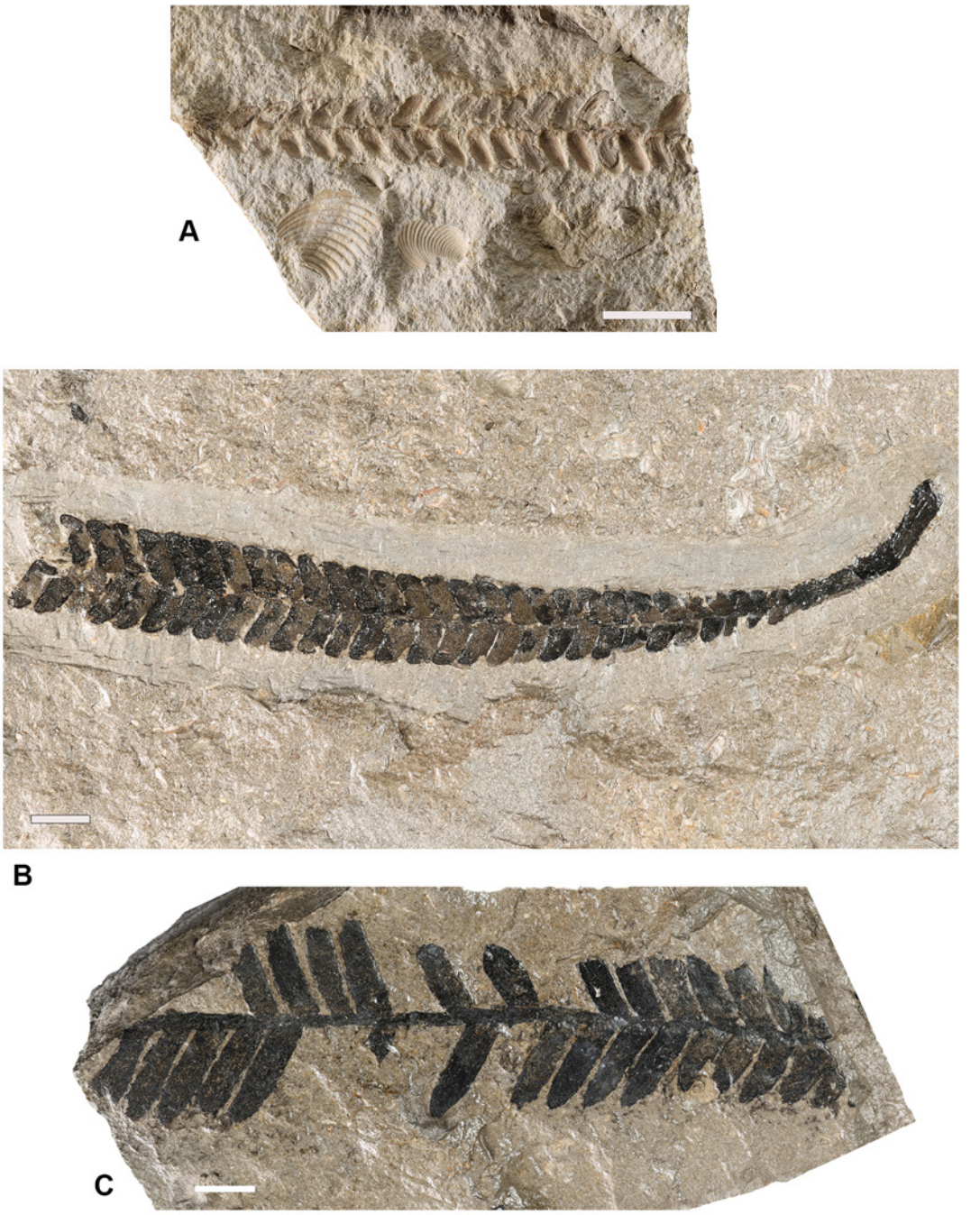


Plate 2: A - *Otozamites reglei* (Brong) Saporta, MNHNL TV049, Ehlerange, Serpentinum Zone, lower Toarcian. B - *Otozamites reglei* (Brong) Saporta, MNHNL TV070, Dudelange, Serpentinum Zone, lower Toarcian. C - *Ptilophyllum pecten* Phillips, MNHNL TV071, Dudelange, Serpentinum Zone, lower Toarcian. Scale bar: 1 cm.

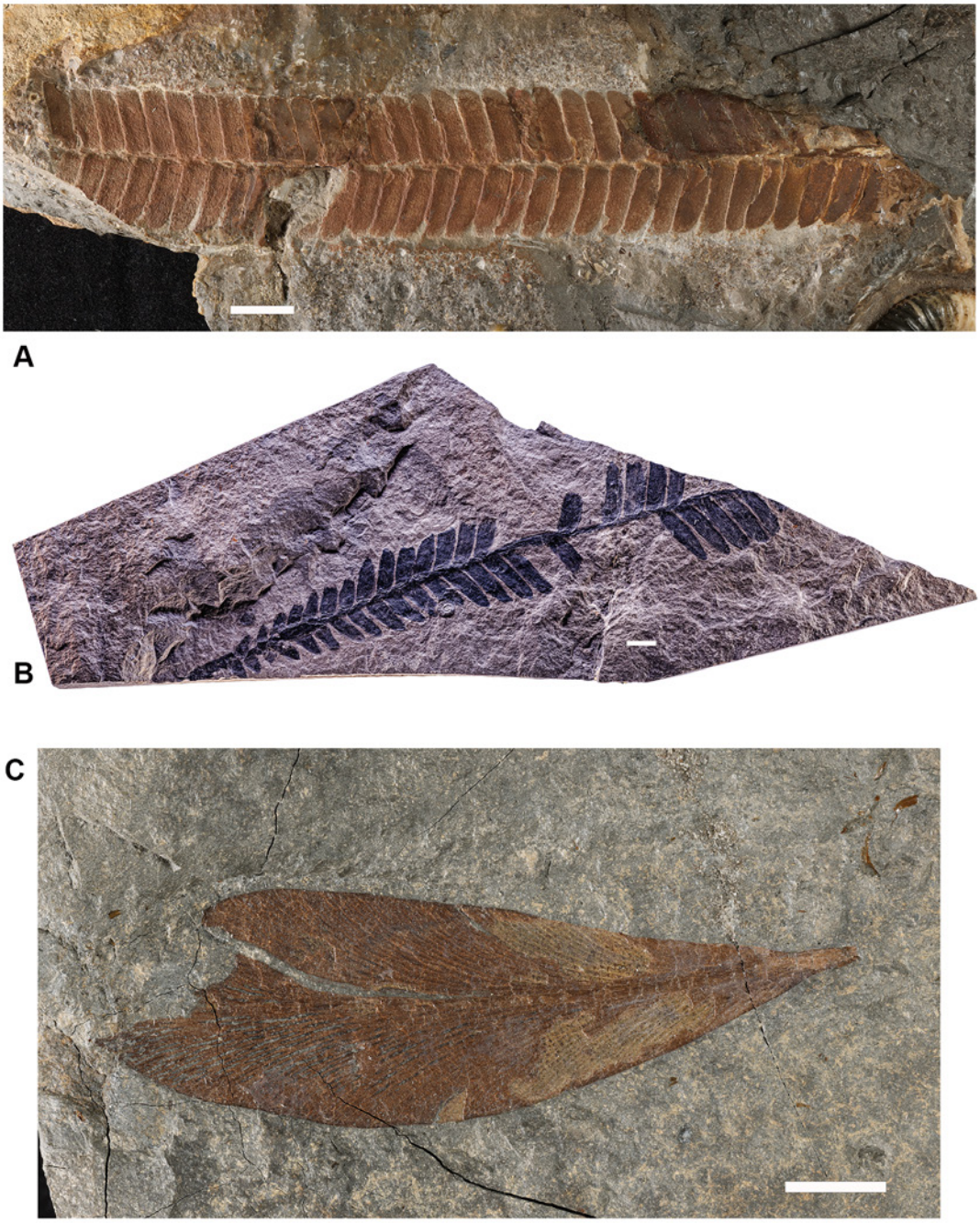


Plate 3: A - *Pterophyllum subaequale* (Hartz) Harris, MNHNL TV048, Soleuvre, Bifrons Zone, lower Toarcian. **B** - *Zamites* sp., MNHNL TU248, Dudelange, Serpentinum Zone, lower Toarcian. **C** - *Sagenopteris phillipsii* Brong., MNHNL TU894, Belvaux, Serpentinum Zone, lower Toarcian. Scale bar: 1 cm.



Plate 4: A - *Ginkgoites* sp., MNHNL TV056, Rodange, Bifrons Zone, lower Toarcian. **B** - *Neocalamites* sp., MNHNL TV308, Foetz, Serpentinum Zone, lower Toarcian. **C** - *Cladophlebis minor* Saporta, MNHNL TV192, Dudelange, Serpentinum Zone, lower Toarcian. Scale bar: 1 cm.

conifers in Mediterranean-type climates (e.g., short, densely packed needle-like leaves).

Within the forest, where a more stable and humid microclimate prevailed, the understory was mostly composed of bennettites, primarily the morphogenera *Otozamites*, *Pterophyllum*, and *Ptilophyllum*.

Tree ferns and seed ferns were poorly represented, which could suggest that these forests were relatively open and not overly dense. In this vegetation, *Equisetopsida, as* representatives of azonal swamp flora, likely inhabited marshy environments. The role and abundance of *Ginkgoopsida* within this vegetation remain unclear.

5 Palaeoflora of the upper Toarcian

So far, only a few fossil specimens from the upper Toarcian have been discovered:

Class: Gymnospermopsida

Ordo: Bennettitales syn. Cycadeoideales

Fam. Williamsoniaceae

Fossil material: compressions and impressions of leaves

Otozamites cf. *thomasii* Harris
Ptilophyllum pecten Phillips
Ptilophyllum sp.
Pterophyllum sp.

These limited findings do not allow for a detailed reconstruction of upper Toarcian vegetation. However, they suggest that bennettites very similar to those from the lower Toarcian were also present during the upper Toarcian. This allows us to cautiously assume that the overall vegetation did not change significantly during this relatively short interval of time (the entire Toarcian lasted approximately 10 million years, from ~184 to ~174 Ma), despite the occurrence of the Toarcian Oceanic Anoxic Event (T-OAE; Suan et al. 2008, among others).

6 Conclusion

During the Toarcian, the shores of the then-existing Tethys Ocean in the studied area were covered by zonal forest vegetation composed predominantly of gymnosperms. The flora was dominated by conifers, mostly *Widdringtonites* and *Pagiophyllum,* and bennettites, mostly *Otozamites*, *Ptilophyllum*, and *Pterophyllum*, whereas representatives of Ginkgoopsida were only rarely present. Notably, Pteridospermales (seed ferns) also occurred, probably as relict species persisting from an earlier stage in vegetation history.

7 Acknowledgements

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Appendix: List of fossil plant specimens

LOWER TOARCIAN

Taxon	Inventory number	Note
EQUISETOPSIDA		
Equisetites sp.	TV188	
Neocalamites elegantulus Maubeuge	TU336	
Neocalamites sp.	TV329, TU209, TV308	
Equisetum sp.	TV489	
POLIPODIOPSIDA - TREE FERNS		
Cladophlebis minor Saporta	TV192, TV282	
PTERIDOSPERMALES - SEED FERNS		
Sagenopteris phillipsii Brong	TU894	Revised from Magnoliaceae
GINKGOALES		
Ginkgoites sp.	TV056	
BENNETTITALES syn. CYCADEOIDEALES		
Otozamites cf. *thomasii* Harris	TV193, TV311	
Otozamites reglei (Brong) Saporta	TV070, TV049	
Pterophyllum subaequale (Hartz) Harris	TV048, TV540	Revised from : TV048 *Ptilophyllum pecten*; TV540 *Otozamites* sp.
Ptilophyllum pecten Phillips	TV071	Revised from *Otozamites* sp.
Ptilophyllum sp.	TV541, TV333	Revised from *Otozamites* sp.
Zamites sp.	TU248	Revised from *Ptilophyllum* sp.
CONIFERALES		
Brachiophyllum sp.	TV537	
Dadoxylon sp.	TU227	Syn. *Agatoxylon*
Pagiophyllum kurri (Schimper) Salfeld	TU305, TV240, TV069, TV169, TV240	
Pagiophyllum cf. *kurri* (Schimper) Salfeld	TV388	
Pagiophyllum sp.	TV335	
Widdringtonites liasinus Kurr.	TV229	
Widdringtonites reichii Ett.	TV314, TV336, TV934, TU419, TU852, TU219, TU605	TU605 revised from *Araucaria* sp.;
Widdringtonites sp.	TV977	
Cupressaceae cf. *Widdringtonites*	TV936	Strobilus and megastrobilus
Coniferales aff. *Frenelopsis*	TV332	
Coniferales gen. et sp. indet.	TV328, TV330, TV331, TV366	
foss. wood, gen. et sp. indet.	TV343, TU156; TU233; TU307; TU423, TU424, TU533, TU659, TU543, TU902, TU909, TU928,	
Plant detritus indet.	TV126, TV127, TV128, TV132, TV189, TV190, TV471, TV473, TV499, TV547, TV569, TV596, TU265, TU845, TU803	

UPPER TOARCIAN

Taxon	Inventory number	Note
BENNETTITALES syn. CYCADEOIDEALES		
Otozamites cf. *thomasii* Harris	TO110	
Ptilophyllum pecten Phillips	TO112	
Pterophyllum sp.	TO111, HO118	
Pterophyllum cf. *subaequale* (Hartz) Harris	DOU229	

Toarcian shark and ray faunas (Chondrichthyans) from Luxembourg and Belgium in the aftermath of the T-OAE

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Keywords: Lower Jurassic, Bifrons-Thouarsense zones, "Couches à Crassum", Dudelange-Zoufftgen, Halanzy, Chondrichthyes, Elasmobranchii, Orectolobiformes.

Abstract

The systematic washing and sorting of sediments from various levels of the Toarcian (upper part of the Bifrons Zone to Thouarsense Zone) from Dudelange-Zoufftgen, Luxembourg, yielded an abundant vertebrate microfauna, dominated by isolated teeth of sharks and rays, warranting comparison with previously described records from so-called 'Couches à Crassum' (Bifrons/Variabilis zones) of Halanzy, Belgium. The two localities share the presence of batomorph Toarcibatidae, in particular *Cristabatis* and *Toarcibatis*, and the dominance of orectolobiforms. New taxa are identified among the Orectolobiforms: *Thiesoscyllium underwoodi,* nov. gen. nov. sp. from the Halanzy locality and *Palaeobrachaelurus vanessae* nov. sp. from both localities. The genus *Thiesoscyllium* comprises a second species from the Bajocian of Luxembourg that is introduced herein: *Th. felteni* nov. sp., previously described as "aff. *Palaeobrachaelurus mussetti*". Furthermore, we attribute the species *Heterodontus duffini* Thies, 1983 to a new orectolobiform genus, *Eoscyllium*, reminiscent of the Hemiscylliidae *Chiloscyllium*. Most of this 'Lorraine-type' shark- and ray-fauna, typically appearing at the top of the Bifrons Zone in Lorraine, northeastern France and adjacent regions in Luxembourg and Belgium, was already established from the Serpentinum Zone in Normandy, northern France.

Schlüsselwörter: Unterjura, Bifrons-Thouarsense Zonen, "Couches à Crassum", Dudelange-Zoufftgen, Halanzy, Chondrichthyes, Elasmobranchii, Orectolobiformes.

Zusammenfassung

Das systematische Waschen und Sortieren von Sedimenten aus verschiedenen Schichten des Toarciums (vom oberen Teil der Bifrons-Zone bis zur Thouarsense-Zone) aus Dudelange-Zoufftgen, Luxemburg, ergab eine reichhaltige Wirbeltier-Mikrofauna, die von vereinzelten Zähnen von Haien und Rochen dominiert wurde und einen Vergleich mit zuvor beschriebenen Funden aus den sogenannten "Couches à Crassum" (Bifrons-/Variabilis-Zonen) von Halanzy, Belgien ermöglicht. An beiden Fundorten kommen batomorphe Toarcibatidae vor, insbesondere *Cristabatis* und *Toarcibatis*, und es überwiegt der Anteil an Orectolobiformen. Unter den Orectolobiformen werden neue Taxa identifiziert: *Thiesoscyllium underwoodi,* nov. gen. nov. sp. von der Fundstelle Halanzy und *Palaeobrachaelurus vanessae* nov. sp. von beiden Fundstellen. Die Gattung *Thiesoscyllium* umfasst eine zweite Art aus dem Bajocium von Luxemburg, die hier vorgestellt wird: *Th. felteni* nov. sp., zuvor beschrieben als "aff. *Palaeobrachaelurus mussetti*". Darüber hinaus ordnen wir die Art *Heterodontus duffini* Thies, 1983 einer neuen Orectolobiform-Gattung zu, *Eoscyllium*, die an die Hemiscylliidae-Gattung *Chiloscyllium* erinnert. Der Großteil dieser Haifisch- und Rochenfauna vom "Lothringer Typ", die üblicherweise im oberen Bereich der Bifrons-Zone in Lothringen, Nordostfrankreich und angrenzenden Regionen in Luxemburg und Belgien vorkommt, konnte bereits in der Serpentinum-Zone in der Normandie, Nordfrankreich, nachgewiesen werden.

Mots clés: Jurassique inférieur, zones à Bifrons-Thouarsense, couches à Crassum, Dudelange-Zoufftgen, Halanzy, Chondrichthyes, Elasmobranchii, Orectolobiformes.

Résumé

Le lavage et le tri systématiques des sédiments provenant de différents niveaux du Toarcien (de la partie supérieure de la zone Bifrons à la zone Thouarsense) de Dudelange-Zoufftgen, au Luxembourg, ont permis de mettre au jour une microfaune vertébrée abondante, dominée par des dents isolées de requins et de raies, ce qui justifie une comparaison avec les données précédemment décrites provenant des " Couches à Crassum " (zones à Bifrons/Variabilis) d'Halanzy, en Belgique.

Les deux sites ont en commun la présence de Toarcibatidae batomorphes, en particulier *Cristabatis* et *Toarcibatis*, ainsi que la prédominance d'orectolobiformes. De nouveaux taxons sont identifiés parmi les orectolobiformes : *Thiesoscyllium underwoodi,* gen. nov. sp. nov. , provenant du site d'Halanzy et *Palaeobrachaelurus vanessae* sp. nov. provenant des deux sites. Le genre *Thiesoscyllium* comprend une deuxième espèce du Bajocien du Luxembourg qui est présentée ici : *Th. felteni* sp. nov., précédemment décrite comme " aff. *Palaeobrachaelurus mussetti* ". De plus, nous attribuons l'espèce *Heterodontus duffini* Thies, 1983 à un nouveau genre d'orectolobiformes, *Eoscyllium*, rappelant les Hemiscylliidae *Chiloscyllium*. La majeure partie de cette faune de requins et de raies de " type lorrain ", apparaissant généralement au sommet de la zone Bifrons en Lorraine, dans le nord-est de la France et dans les régions adjacentes du Luxembourg et de la Belgique, est déjà présente à partir de la zone à Serpentinum en Normandie, dans le nord de la France.

1 Introduction

In the Toarcian of the north-eastern margin of the Paris Basin (French and Belgian Lorraine, Grand-duchy of Luxembourg), the condensation horizon between the top of the Tenuicostatum Zone and the base of the Serpentinum Zone yields an abundant and diverse shark microfauna: rare teeth of *Hybodus* sp., abundant and diverse Synechodontiforms (aff. *Rhomphaiodon*, *Palidiplospinax* cf. *occultidens*, *Palidiplospinax* cf. *enniskilleni*, and the Pseudonotidanidae *Welcommia terencei* Delsate & Godefroit, 1995 (see Klug & Kriwet 2010). Occurences of shark remains are rare between this horizon and the Crassum Subchronozone (top of Bifrons to base of Variabilis Zones), except for the Hybodontiforms *Hybodus hauffianus* Fraas, 1895 from the bituminous shales of the Serpentinum Zone and the marls and limestones of the Bifrons Zone, *Hybodus* sp. and *Hybodus grossiconus* from the marls of the Bifrons Zone (Delsate 1992, 1993, 1995, 1997), and a hybodont fin spine cf. *Hybodus hauffianus* from the Bifrons Zone of Soleuvre (Delsate 199: Pl.1 fig.3; MnhnL collection n° Ti001).

The Halanzy locality (Delsate & Lepage 1990; Delsate & Thies 1995; Thies 1993; Delsate & Candoni 2001, 2002; Delsate & Weis 2010) is dated to the Crassum Subzone. The so-called 'Crassum bed' corresponds to a lumachellic, marly or indurated phosphatic level, a condensation horizon between the top of the Bifrons Zone and the base of the Variabilis Zone (see Delsate & Weis 2010).The Dudelange-Zoufftgen section (Table 1) (Delsate & Weis 2010) yields teeth of actinopterygian fish and chondrichthyans from the base of the Crassum Subzone (Level 4 in Delsate & Weis 2010), with greatest abundance and species richness in sharks and rays (mostly Orectolobiforms) occurring in the Thouarsense Zone (level 11 in Delsate & Weis 2010).

2 Material & methods

The location and biostratigraphy of the Dudelange-Zoufftgen section is reported in Delsate & Weis (2010), and the coordinates of the Halanzy site in Delsate & Thies (1995). The teeth mentioned, described or illustrated in the present paper are deposited in the palaeontological collections of the National Museum of Natural History of Luxembourg (acronym: MnhnL) and the Royal Belgian Institute of Natural Sciences of Brussels (acronym: RBINS).

After size reduction and drying, the sediments were soaked in hot water with soapy surfactant for the clays, hydrogen peroxide (10 %) for the marls, or acetic acid (10 %) for the limestones, then carefully washed over sieves of 2 and 0.3 mm mesh size respectively using warm water. After drying of the residues, picking and sorting were performed under stereomicroscope. Photographs were taken with Keyence VHX-6000 optical microscope, or with the SEM Neoscope JCM-5000 of MnhnL. Some photos were taken using the SEM of Royal Belgian Institute of Natural Sciences of Brussels by Mr Julien Cillis, and using the SEM of Trier University by Mrs Emma Krings.

3 Systematic Palaeontology

We follow the classification and teeth description of Cappetta (2012) and Klug & Kriwet (2010, 2018) for the Synechodontiformes. We use the terms:

Apron: for a labial and mesio-distally complete basal expansion of the crown over the root.

Labial crown apophysis: for a labial and mesio-distally restricted, basal expansion of the crown over the root.

Labial apronal protuberance: for an apophysis or protuberance developed on the expanded base (apron) of the crown.

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Order Hybodontiformes Maisey 1975
Superfamily Hybodontoidea Owen 1846

Hybodontoidea indet.

Pl. 1 B

2010 Hybodontidae indet. – Delsate & Weis: pl. 6, fig. 1.

Material – one dermal denticle from the Thouarsense-Bingmanni Subzone of Dudelange-Zoufftgen, MnhnL TM225.

Description - The dermal denticle from the Thouarsense-Bingmanni Subzone is stud-shaped, with a circular base and a single crown with a diameter of 0.5 mm. It is similar to the "Type 2 Scales - Hybodontoids, Groupe a" in Delsate et al. (2002; fig. 17, pl. 10, fig. A).

Occurrence - Hybodontoidea: from Paleozoic to Upper Cretaceous (Maastrichtian).

Family Hybodontidae Owen 1846

Genus *Hybodus* Agassiz 1837

Hybodus sp.

Pl. 1 A

Material - Two dental fragments from the Couches à Crassum of Halanzy, MnhnL TM541a, b.

Description - Although Delsate *et al* 1989 & Delsate & Lepage 1990 did not initially report Hybodontids from the Couches à Crassum at Halanzy, this level turned out to yield 2 fragments of Hybodontidae: a 5 mm high broken crown (MnhnL TM541; figured in Pl.1 A) is ornamented by fine ridges, denser at the base of the crown, it preserved one sharp mesio-distal carina. The second fragment is a broken crown heel with two lateral cusplets ornamented by ridges (not figured). These fragments are probably attributable to the genus *Hybodus* Agassiz 1837.

Occurrence - The genus *Hybodus* occurs in the Middle Triassic to the Upper Cretaceous (Maastrichtian) of Europe, North America, northern and western Africa, and Asia (Cappetta 2012).

Subcohort Neoselachii Compagno, 1977
Incerti superordinis
Order Synechodontiformes Duffin and Ward, 1993
Family Palaeospinacidae Regan, 1906

Genus *Palidiplospinax* Klug & Kriwet, 2008

Palidiplospinax enniskilleni (Duffin & Ward, 1993)

Pl. 1 C-I

1989 *Palaeospinax* sp - Delsate et al. 1989: fig. 1.

1990 Palaeospinacidé, dent latérale, vue labiale - Delsate & Lepage : fig. 1.

1995 *Synechodus* cfr *enniskilleni* - Delsate & Godefroit.

2010 *Synechodus* cf. *duffini* Underwood & Ward, 2004 - Delsate & Weis, pl. 6, fig. 2.

Material - 5 teeth and several fragments (MnhnL TM226 – TM542 - TM543) from Dudelange-Zoufftgen level 11 (Thouarsense zone, Thouarsense-Bingmanni subzones); 10 teeth and fragments from Halanzy (Couches à Crassum) including one posterior tooth (MnhnL TM544), in lingual, labial, occlusal and basal views.

Description - *Palidiplospinax enniskilleni* (Duffin and Ward, 1993) shows a strong monognathic heterodonty, with high upright prehensile anterior teeth distally inclined anterolateral (MnhnL TM542 : Pl 1 G, preserved width 1.5 mm) , lateral teeth (Pl 1 I, MnhnL TM226, mesio-distal width 3 mm) with 2 distal and 3 mesial cusplets, elongated crushing postero-lateral (MnhnL TM543 : Pl 1 H, mesio-distal width 2 mm) and posterior teeth (Pl 1 C-F, MnhnL TM544, mesio-distal width 3.8 mm) with a low coronal profile with a lower central cusp and lateral cusplets. The central cusp and the lateral cusplets are usually well ornamented. Labial vertical ridges ascend the crown from a longitudinal ridge and generally reach the occlusal crest and the cusp apices; they may bifurcate basally. The root of the anterior teeth is of synechodontiform (pseudopolyaulacorhize) type. The root of the posterior tooth (Pl 1C-F) is very elongated. A series

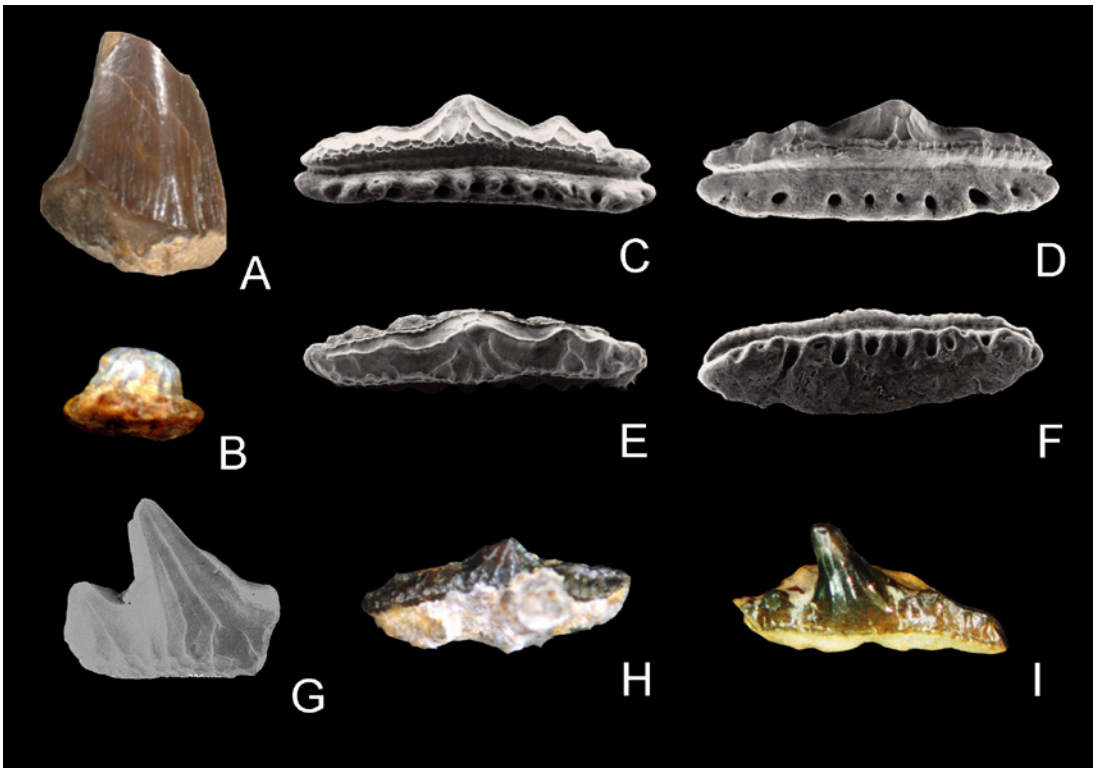


Plate 1: *Hybodus* and *Palidiplospinax*. **A** - TM541, *Hybodus* sp: fragment of the main cusp, preserved height: 5 mm; Halanzy, Couches à Crassum. **B** - TM225, Hybodontoidea dermal denticle, diameter 0.5 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones). **C-F** - TM544, *Palidiplospinax* cf. *enniskilleni* (Duffin & Ward, 1993): posterior tooth, **C** - labial view, **D** - lingual view, **E** - occlusal view, **F** - basal view; mesio-distal width 3.8 mm; Halanzy, Couches à Crassum. **G** - TM542, *Palidiplospinax enniskilleni*, fragment of anterolateral tooth, preserved width 1.5 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones). **H** - TM543, *Palidiplospinax enniskilleni* (Duffin & Ward, 1993), mesio-distal width 2 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones). **I** - TM226, *Palidiplospinax enniskilleni* (Duffin & Ward, 1993), mesio-distal width 3 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones).

of nine well-marked nutritive grooves of various diameters pierce its labial face, incising the labial part of the basal plate. Nine corresponding smaller foramina of various sizes pierce the lingual face of the root, without incising the lingual part of the basal plate.

Occurrence - Lower Lias (Sinemurian?) of England (Duffin & Ward, 1993), Sinemurian of Belgium (Delsate & Duffin 1993), Pliensbachian of Grimmen, north-eastern Germany, (Stumpf & Kriwet 2019 Pl 3 a-b), and Upper Toarcian of Belgium (Couches à Crassum) and Luxembourg (Dudelange-Zoufftgen, Crassum-Schichten (levels 4-5) to Thouarsense zone (level 11).

Superorder Squalomorphii? Compagno, 1973
Family Protospinacidae Woodward, 1918

Genus *Protospinax* Woodward, 1918

Protospinax cf. *magnus* Underwood & Ward, 2004

Pl. 2 A-H

1990 *Protospinax* sp. (vue labiale d'une dent latérale) - Delsate & Lepage: Fig. 3B.

2010 *Protospinax magnus* Underwood & Ward, 2004 - Delsate & Weis: Pl. 6, fig. 3.

Material - 30 teeth including MnhnL TM227 and TM545 (the mesio-distal width of both is 1 mm) from Dudelange-Zoufftgen, Crassum-Schichten

(levels 4-5) to Thouarsense zone (level 11); 20 teeth from Halanzy, Couches à Crassum (MnhnL TM546, TM547, TM548, TM549) .

Description - Three morphotypes of *Protospinax* are present:

- Anterior teeth (Pl 2 A, B, C), tall, (MnhnL TM545 (Pl. 2A), MnhnL TM546 (Pl. 2B, C), mesio-distal width 1.0 mm; with a central cusp and one or two pairs of lateral cusps (generally all abraded by functional wear); V-shaped root, hemiaulacorhize, with a central foramen at the junction of the 2 lobes,
- Smaller teeth (MnhnL TM547: Pl 2 D) with low cusps, one low and usually abraded main cusp and 2 accessory, very low cusplets, often also abraded, with a thin triangular uvula, a V-shaped root with a central foramen,
- Lateral and postero-lateral teeth: MnhnL TM548 (Pl. 2E) lateral tooth, MnhnL TM549 (Pl. 2 F,H), MnhnLTM227 (Pl. 2G) postero-lateral teeth, lower and elongated mesio-distally (the mesio-distal width of MnhnL TM 227 (Pl. 2G), is 1 mm), with a single small, very eccentric, low cusp (Pl. 2 E, F, G, H). Their root has the shape of a very obtuse V, without a furrow, nearly a straight bar, keeping a visible eccentric foramen,

Discussion - The teeth Pl 2 A-C described herein strongly resemble the very heterodont *P. magnus* Underwood & Ward 2004 from the English Bathonian, on account of the development and number of the cusps with the well-developed main cusp, the well-defined 4 accessory cusplets on the anterior teeth, the elongated oval shape of the posterior teeth (Pl. 2 E,F,G,H) with the eccentric preservation of the small inclined main cusp, and the root varying from elongated bar (Underwood & Ward 2004 Pl 11:8) to V shaped hemiaulacorhize (Underwood & Ward 2004 Pl 11:5). The tooth Pl 2 D evokes *P. magnus* P6619 (Underwood & Ward 2004, Pl 11: 9-11), a small anterolateral (or possibly juvenile) tooth.

The material from the Toarcian of Halanzy and Zoufftgen differs from *Protospinax annectans* Woodward 1918, that possesses a strongly concave labial face of the crown, and a nutritive groove separating the lobes of the root, from *P. annectans* from the British Callovian described by Thies (1983) that has a pointed main cusp, two faint accessory cusps disappearing on laterals, a very moderately concave labial face of the crown, and a V shaped root, from *P. planus* Underwood 2002 from the Kimmeridgian of Ringstead that shows only a poorly developed main cusp, with faint or absent accessory cusps and a very flat labial face of the crown, from *P. bilobatus* Underwood & Ward 2004 that shows a bilobate root with prominent nutritive groove, and low lateral cusplets, from *Protospinax carvalhoi* Underwood & Ward, 2004 that shows a low degree of heterodonty, a rhombic crown in labial view, a stronger bulbous uvula, a short blunt main cusp, incipient or absent lateral cusplets, and a slightly concave basal edge of the apron, and from *P. lochensteinensis* Thies 1983: 94 pl. 4 figs 1-6 from the German Oxfordian that shows a low (and very faint on postero-lateral positions) main cusp, faint or absent accessory cusps, a very rounded labial face of the crown of the anterior teeth, and a median tubercle or button or a vertical ridge directed to the main cusp on the labial face of all the positions .

Remarks - To differentiate the anterior and antero-olateral positions of *Protospinax* from those of Orectolobiforms, which can be morphologically similar in the arrangement of the cusps (mostly in Hemiscylliidae), we propose the following keys:

- absence (in *Protospinax*) or presence (in some Orectolobiforms) of a well-marked rectangular or rounded apophysis, or protuberance, at the labial base of the crown, that we consider as a synapomorphy (derived character shared by the whole group considered) for the whole Orectolobiforms + Batomorphs + Squatinomorphs. The absence of a basal crown protuberance does not exclude an orectolobiform attribution; the protuberance can be rectangular or rounded, high or low, varying with the heterodonty, or absent for example in Hemiscylliidae.
- the heterodonty of *Protospinax magnus* sees a disappearance of the lateral cusps, from the front of the mouth towards the back, unlike the heterodonty of the Orectolobiforms, and a strong increase in the ratio 'mesio-distal width of the crown / total height of the crown'.

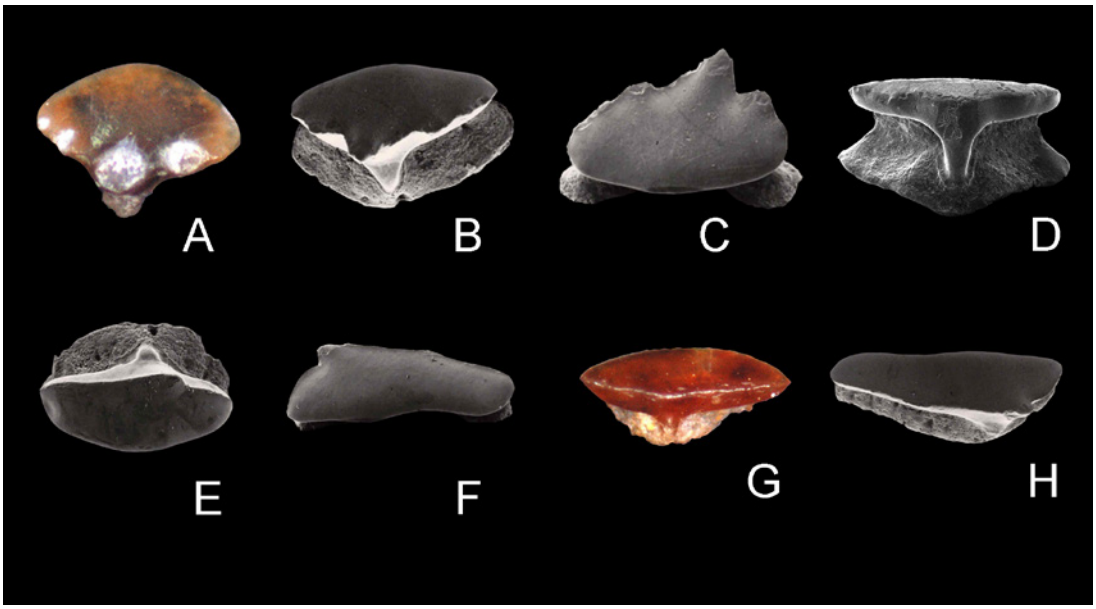


Plate 2: *Protospinax* cf. *magnus* Underwood & Ward 2004. **A** - TM545, antero-lateral tooth, mesio-distal width 1.0 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones). **B-C** - TM546, antero-lateral tooth, **B** - apical view, **C** - labial view; mesio-distal width 0.77 mm, lingual oblique view (same tooth as 2C); Halanzy, Couches à Crassum. **D** - TM547, anterolateral tooth, lingual view mesio-distal width 0.81 mm; Halanzy, Couches à Crassum. **E** - TM548, lateral tooth, mesio-distal width 0.89 mm; Halanzy, Couches à Crassum. **F-H** - TM549, posterior tooth, **F** - labial view, **H** - apical view; mesio-distal width 1.5 mm; Halanzy, Couches à Crassum. **G** - TM227, posterior tooth mesio-distal width 1.0 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones).

- in *Protospinax*, the uvula usually starts immediately, and more perpendicular, at the apical top of the lingual face of the main cusp or crown. In *Palaeobrachaelurus*, the uvula begins lower near to the base of the lingual face of the crown. This is evident in *Protospinax annectans* Woodward 1918 (see Thies 1983: 92 & 93: Pl.3 figs 2-6, and *Protospinax lochensteinensis* Thies 1983: 94 pl. 4 figs 1-6.

As an example, these 3 points allow to discard the taxon *Pseudospinax muftius* (Thies 1983) (Callovian of Rookery Pit, UK) from a *Protospinax* affinity and to place it in Orectolobiforms, in agreement with Underwood and Mitchell (1999), because of the higher uvula, the V-shaped root. Within the Orectolobiforms, *P. muftius* does not seem to belong to the elongated mesio-distally Palaeobrachaeluridae, but rather to the Hemiscylliidae, because of the absence of the diagnostical expanded mesial and distal wings, the shape and position of the uvula, the rounded labial apron, the possession of just one pair of small cusplets, symmetrical or asymmetrical with monognathic heterodonty. It compares well to *Pseudospinax heterodon* Underwood & Mitchell 1999: p. 20-22 & Pl 5, Fig 3-10 from the Albian of Northeast England.

Müller & Diderich (1991) introduced the genus *Pseudospinax* in the Orectolobiformes *familia incertae* with the species *Pseudospinax pusillus* (pl. 17, fig. 1 abc, holotype 120605) and distinguished it from Protospinacidae on the base of its hemiaulacorhize root, although various *Protospinax* species may have hemiaulacorhize roots (Underwood & Ward 2004: 483), for example *P. magnus* Underwood & Ward, 2004. Underwood (2002) figures *Pseudospinax* from the Kimmeridgian of Ringstead southern England. Kriwet (2003, fig 2B) attributes one tooth from the Callovian of Kleby to *Pseudospinax*, which differs from *Pseudospinax muftius* and *Pseudospinax heterodon* by its regularly convex basal edge that is deeper than in *Pseudospinax muftius*, *P. pusillus* or *P. heterodon*.

I agree with Underwood & Mitchell (1999: 21) stating about *Pseudospinax* that "Species probably referable to this genus include *Protospinax? muftius* Thies, 1983 from Callovian clays of Southern England,...", and Rees (2010: 896), "This poorly known genus has previously been recorded in the Middle Jurassic of Germany (*Pseudospinax muftius* (Thies, 1983), see Underwood (2002)) and in the Callovian of Poland (Kriwet 2003)".

Underwood and Mitchell (1999) place *Pseudospinax* in Hemiscylliidae, as I propose for *Eoscyllium* nov. gen., based on functional wear of the cusps that is absent or minimal in Orectolobiformes, but very marked (and often on several cusps) in *Protospinax*, suggesting a generalist diet with a strong grinding component, and on other less exclusive criteria such as the very convex section of the main cusp and its extension towards the apron in Orectolobiformes (this section is barely convex in *Protospinax*), the shape of the root, the "cuspidity" index (% height of the main cusp / total height of the crown), and the "basality" index (% height of the crown under the largest mesio-distal axis / total height of the crown).

Occurrence - Upper Toarcian, Couches à Crassum of Halanzy, and Couches à Crassum (levels 4-5) to Thouarsense zone (level 11) of Dudelange-Zoufftgen; Bathonian of the United Kingdom.

Super Order Galeomorphii Compagno, 1973
Order Heterodontiformes Berg, 1937
Family Heterodontidae Gray, 1851

Genus *Paracestracion* Koken in Zittel, 1911

Paracestracion sarstedtensis (Thies, 1983) [Underwood, 2002]

Pl. 3

1989 *Heterodontus* sp. - Delsate et al.: fig. 6.

1990 Heterodontus cfr *sarstedtensis* Thies 1983 - Delsate & Lepage: fig. 2A & 2B.

2010 *Paracestracion sarstedtensis* (Thies, 1983) Underwood, 2002 - Delsate & Weis: Pl. 6, fig. 4.

Material - 5 teeth including MnhnL TM228 (Pl. 3 Fig. F) (Delsate & Weis 2010: Pl. 6, fig. 4) and MnhnL TM554 from Zoufftgen (Zone à Thouarsense, sous-zone à Thouarsense-Bingmanni), and 20 teeth from Halanzy, Couches à Crassum (including MnhnL TM550, TM551, TM552, TM553).

Description - The crowns of *P. sarstedtensis* generally bear five to seven subequal cusps and lack a true uvula. The long axis of the basal plate is significantly smaller than that of the crown. The mesio-distal width ranges from 0.45 mm (MnhnL TM550) to 1.1 mm (MnhnL TM228 and TM554), just like the Holotype (1.1 mm) and Paratype (0.5 mm) in Thies 1983.

Occurrence - Upper Toarcian, Couches à Crassum at Halanzy; levels 6 (Variabilis zone, Illustris and Variabilis subzones), 8 (Thouarsense zone, Thouarsense and Bingmanni subzones), and 11 (Thouarsense zone, Thouarsense and Bingmanni subzones) of Dudelange-Zoufftgen; Upper Aalenian of Moorberg, Germany (Thies 1983).

Super Order Galeomorphii Compagno, 1973
Order Orectolobiformes Applegate, 1974
Family Brachaeluridae Applegate, 1974

Genus *Palaeobrachaelurus* Thies, 1983

Remark - This genus is known from the Upper Toarcian – Lower Aalenian of Moorberg (Germany) (*P. aperizostus* Thies, 1983), from Great Britain in the Bathonian (*P. musseti* Underwood, 2002) and the Callovian (*P. alisonae* Thies, 1983; *P. bedfordensis* Thies, 1983). *Palaeobrachaelurus* is defined by a V-shaped ("hemiaulacorhize") root, a crown broadened mesio-distally by the presence of 2 wings or arms ("flügelartig verbreitert") bearing the accessory cusplets, a high main cusp, an uvula, and an apron with a variously developed labial protuberance (from a slight superimposed convexity to a strong rectangular peg) .

Palaeobrachaelurus cf. *aperizostus* Thies, 1983

Pl. 4

2010 *Palaeobrachaelurus aperizostus* Thies 1983 – Delsate & Weis: pl. 6, fig. 5.

Material - 7 teeth from Zoufftgen Level 11 (Thouarsense zone, Thouarsense and Bingmanni sub-zones) of Dudelange-Zoufftgen, including TM229, and 3 specimens (MnhnL TM555, 556 & 557) from the Couches à Crassum of Halanzy.

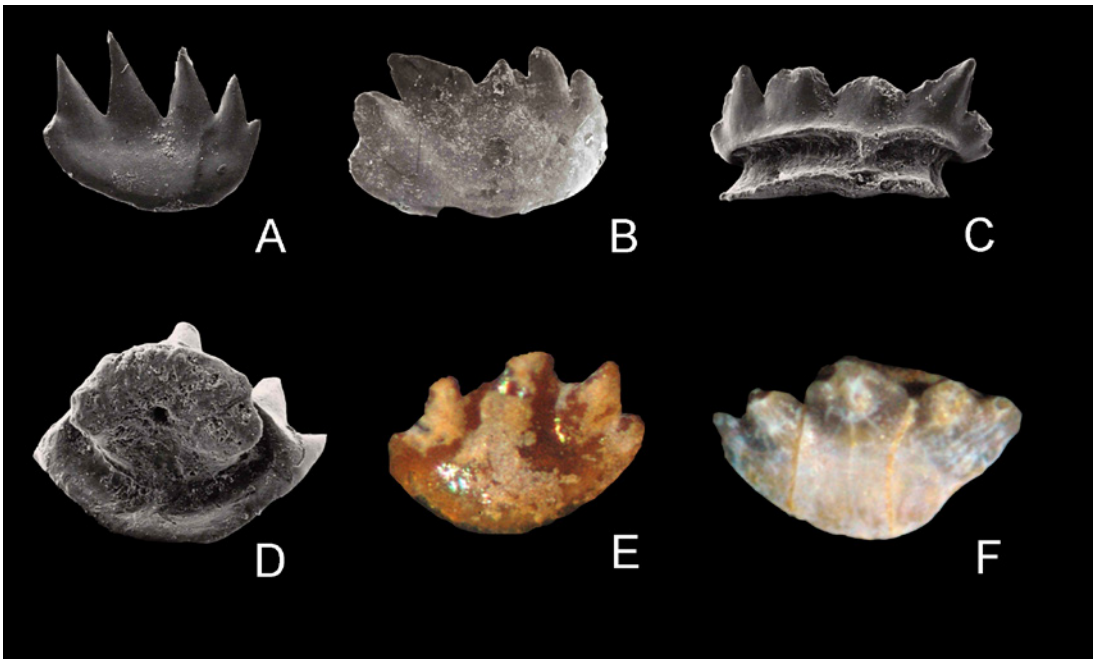


Plate 3 - *Paracestracion sarstedtensis* (Thies 1983). A - TM550, labial view, mesio-distal width 0.45 mm; Halanzy, Couches à Crassum. B - TM551, labial view, mesio-distal width 0.71 mm; Halanzy, Couches à Crassum. C - TM552, lingual view, mesio-distal width 0.6 mm; Halanzy, Couches à Crassum. D - TM553, basal view, mesio-distal width 0.53 mm; Halanzy, Couches à Crassum. E - TM554, labial view, mesio-distal width 1.1 mm; Zoufftgen Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). F - TM228, labial view, mesio-distal width 1.1 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones).

Description - *Palaeobrachaelurus* bearing two pairs of lateral cusps separated by sharp incisions, with a well-marked labial protuberance of the apron, not rectangular but simply convex. The root is V-shaped with a lingual lobe, hemiaulacorhize, with a central labial foramen in the angle of the V, and a medio-lingual foramen at the lingual face of the root lobe. The medio-distal width ranges from 0.8 mm (TM556, PL. 4 C) to 1.7 mm (TM229, Pl. 4 E, F, G, H).

Remark - We use *Palaeobrachaelurus* "cf." *aperizostus* because the uvula is much smaller and thinner in our specimens in comparison with *Palaeobrachaelurus aperizostus* Thies 1983 from the Upper Toarcian and Aalenian of Moorberg.

Occurrence - *Palaeobrachaelurus* cf. *aperizostus* Thies, 1983 occurs in Level 11 (Thouarsense zone, Thouarsense and Bingmanni sub-zones) of Dudelange-Zoufftgen; although *P.* cf. *aperizostus* was not reported in the preliminary papers of Delsate et al. (1989) and Delsate & Lepage (1990), it turned out to occur in the Couches à Crassum of Halanzy (3 specimens) along with the more abundant *P.* cf. *alisonae* (about 240 specimens). *Palaeobrachaelurus aperizostus* (Thies 1983) occurs in the Upper Toarcian and Aalenian of Moorberg, Germany.

Palaeobrachaelurus alisonae Thies, 1983

Pl. 5 F

2010 *Palaeobrachaelurus alisonae* Thies 1983 – Delsate & Weis 2010: pl. 6, fig. 6.

Material - 3 specimens from Zoufftgen, including the specimen MnhnL TM230 figured by Delsate & Weis 2010, Fig. 6. (mesio-distal width 1.1 mm), and 12 specimens from Halanzy.

Description - Only few specimens with a high upright main cusp and 2 rather close cusplets may be attributed to *Palaeobrachaelurus alisonae* Thies 1983, known from the Callovian of Rookery Pit, especially to specimen paratype 1 of Thies 1983.

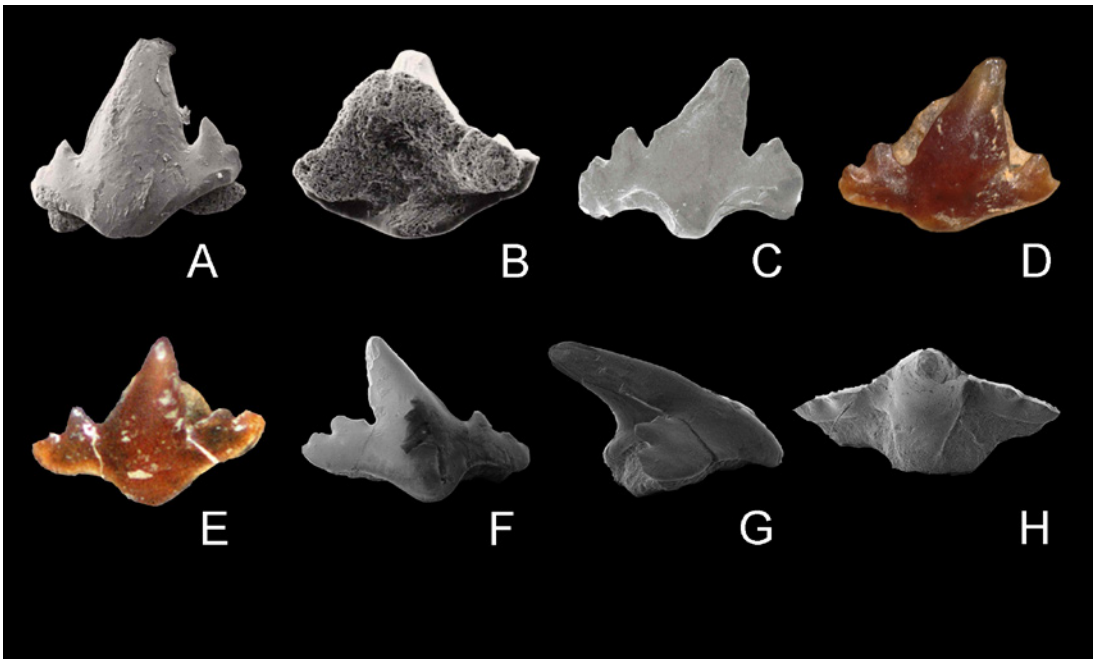


Plate 4: *Palaeobrachaelurus* cf. *aperizostus* Thies 1983. A-B - TM555, A - oblique labial view, B - basal view, mesio-distal width 0.95 mm; Halanzy, Couches à Crassum. C - TM556, labial view, mesio-distal width 0.8 mm; Halanzy, Couches à Crassum. D - TM557, labial view, mesio-distal width 1.3 mm; Halanzy, Couches à Crassum. E-H - TM229, E, F - labial view, G - profile, H - lingual view; mesio-distal width 1.7 mm. F is SEM mirror image of E; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones).

The mesio-distal width is around 1 mm, the total height of the crown is around 1.2 mm. The crown bears a high and robust central cusp, the wings are not very expanded, bearing 2 small hook-like or pyramidal accessory cusps very close to the main one; the labial crown apophysis is rounded or rectangular. The root is V-shaped, with a central foramen opening labially between the 2 arms, with a well-defined lingual lobe, of which the lingual face is incised by a medio-lingual foramen.

Occurrence - Dudelange-Zoufftgen Level 11 (Thouarsense zone, Thouarsense and Bingmanni subzones), upper Toarcian Couches à Crassum of Halanzy; Callovian of Rookery Pit (Great Britain).

Palaeobrachaelurus cf. *alisonae* Thies, 1983

Pl. 5 A-E

1989 *Palaeobrachaelurus* sp. (face externe) - Delsate et al.: pl. 1, fig. 4.

1990 *Palaeobrachaelurus* cfr *alisonae* - Delsate & Lepage: pl. 1, fig 5.

Material - About 240 teeth (including MnhnL TM558, 559, 560) from the Locality Halanzy (Couches à Crassum).

Description and discussion - The genus attribution agrees with the definition ("flügelartig verbreitert") of *Palaeobrachaelurus* by its expanded mesial and distal wings bearing the accessory cusplets.

The mesio-distal width is 0.65 to 1.1 mm. These are well-developed, upright and parallel to the main cusp, which is never very high, giving the teeth a fork-like appearance. The accessory cusplets remain well defined in the supposed more posterior positions, without disappearing of the mesial one. Well-defined labial coronal apophyses are present, rectangular rounded in supposed antero-(lateral) positions, more knob like in posteriors. The uvula is neither long nor wide, it is knob-like and may be laterally limited by small vertical ridges in more posterior positions. The roots have an open-V shape and show two vascularization patterns:

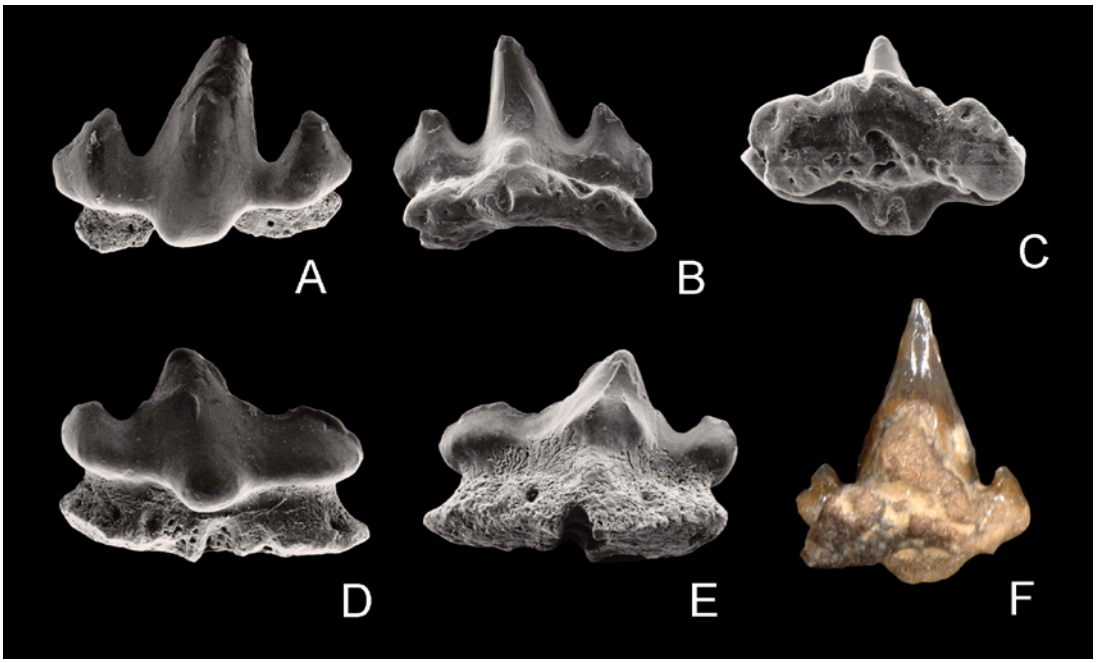


Plate 5: *Palaeobrachaelurus* cf. *alisonae* and *Palaeobrachaelurus alisonae* Thies 1983. **A** - *Palaeobrachaelurus* cf. *alisonae* Thies 1983, TM558, antero-lateral, labial view, mesio-distal width 0.85 mm; Halanzy, Couches à Crassum. **B-C** - *Palaeobrachaelurus* cf. *alisonae* Thies 1983, TM559, antero-lateral, **B** - lingual view, **C** - basal view; mesio-distal width 0.80 mm; Halanzy, Couches à Crassum. **D-E** - *Palaeobrachaelurus* cf. *alisonae* Thies 1983, TM560, postero-lateral, **D** - labial view, **E** - lingual view; mesio-distal width 0.68 mm; Halanzy, Couches à Crassum. **F** - *Palaeobrachaelurus alisonae* Thies 1983 TM230, anterior, lingual view, mesio-distal width 1 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones).

hemiaulacorhize (in antero-(lateral) positions) and holaulacorhize (in more posterior positions).

This material differs from *P.* (cf.) *aperizostus* which shows no clearly defined labial coronal apophysis (just a low convexity than can even be incised), 2 x 2 lateral cusplets (but Paratype 3 only 2 x 1), and a very wide and moderately high uvula, and from *P. bedfordensis* which shows 2 x 2 cusplets and a much higher, longer and wider uvula. Furthermore, our Toarcian material did not provide any morphotype of the posterior-most positions of *P. bedfordensis* (see Thies 1983 Fig. 9-6a, identical to the posterior-most positions of Callovian *P. alisonae* (Thies 1983, Fig. 10 a) except for a wider uvula in *P. bedfordensis*)

The material furthermore differs from teeth of *Akaima* Rees (2010) from the Callovian-Oxfordian of Poland that show a mesio-distally narrow crown with absent lateral cusplets and a median crest restricted to the labial apronal apophysis in anterior teeth, lateral blades or small cusplets on antero-lateral positions, well-developed and strongly divergent lateral cusplets and a median crest that extends onto the labial apron in all lateral teeth, a peg-like to rounded apronal apophysis without concavely indented labial margin, a small and tapering uvula, and a hemiaulacorhize vascularization pattern on all teeth.

It is like the Callovian *P. alisonae* in showing one main and two lateral cusplets. The crown bears only 2 lateral cusplets, well individualized from the main cusp; the holotype and paratypes 1-2 (Thies 1983, Plate 10, figs 1-2-3) show incipient tiny cusplets at the base of the cusplets. There is a very well-defined rectangular to tongue shaped labial apophysis of the crown, remaining well marked on different positions.

Nevertheless, several differences from *P. alisonae* justify the tentative identification as *P.* "cf." *alisonae*: the uvula of the Toarcian *P.* cf. *alisonae* is thinner and narrower than in the Callovian *P. alisonae*, the

lateral cusps are higher and better separated from the main cusp than in the Callovian *P. alisonae*, the cusps are more diamond shaped in the Toarcian *P.* cf. *alisonae* than on the Callovian *P. alisonae*, the main cusp of the Toarcian *P.* cf *alisonae* is never as high and wide than in the Callovian *P. alisonae*, the main cusp of the Callovian *P. alisonae* remains high even in lateral positions, then strongly inclines in the posterior positions, the lateral cusps of the Callovian *P. alisonae* remain well defined on lateral teeth near the distally inclined and still high main cusp, whereas only the posterior-most positions of the Callovian *P. alisonae* see the disappearance of the mesial cusplet (as in *P. bedfordensis*). Our Toarcian material did not provide such a morphology of the posterior-most positions of *Palaeobrachaelurus*.

Remarks - The heterodonty pattern (mostly variations in the height, size and inclination of the cusps) of *Annea maubeugei* Delsate & Thies 1995 is ascertained by the doubtless attribution to one single species, thanks to the diagnostic median keel of the main cusp. Such a heterodontic gradient can be established for the 3 groups of teeth attributed to 1) *Palaeobrachaelurus alisonae* Thies 1983 (3.5% of the Halanzy Toarcian group) representing anterior-most positions (Plate 5F), 2) the Halanzy morph *Paleobrachaelurus* cf. *alisonae* (74.5% of the group) representing anterolateral, lateral and posterolateral positions (Plate 5 A-D), and 3) *Jurobatos cappettai* (22% of the group) representing posterior-most positions (Plate 11 A-F).

This supposed heterodonty leads to introduce the hypothesis of one single taxon including the 3 grouped morphologies. Such a taxon reminded me of the undescribed SMNS 52666 skeleton from the Posidonia Shale Formation of Holzmaden, a very rare complete specimen of Neoselachian, introduced by C. Duffin under the informal name "*Xulagrodon*" (Lecointre et al. 1994), and figured as a batoid by Maisey et al. (2020: 20) in their Squatinid phylogeny paper. I had the opportunity to briefly examine the specimen in the 1990's in Stuttgart with Ronald Böttcher: it rather reminded of an Orectolobiform with a flat rostrum. I thank Chris Duffin and Jürgen Kriwet for allowing me to use elements of their descriptions of their upcoming new genus "*Xulagrodon*", for the sake of comparisons:

Dentition and (monognathic?) heterodonty of "*Xulagrodon*": The mesio-distal width varies from 1 mm in anterior positions to 0.5 mm in posteriors. The central cusp height decreases from very high to subequal to the height of the lateral cusplets. The central cusp is vertical in anterior-most teeth, distally inclined in antero-laterals, then in a more vertical position again in postero-laterals. A median crest extends onto the labial apron (or the apronal apophysis) only in anterior-most teeth, but never in anterolateral or posterolateral position. Additional labial ridges may be present. The labial ornamentation of the crown changes from multiple vertical ridges to a few vertical ridges and then to only one vertical ridge in posterior-most teeth, although this is very variable mostly in antero-laterals. Vertical ridges occur at the base of the lingual face of the crown in some teeth. A single pair of incipient lateral cusplets is present in the anterior teeth, and small rounded, slightly divergent lateral cusplets are present on the mesio-distally extended heels of the lateral teeth. The lateral cusplets, when developed, lack any ornamentation. The labial coronal apophysis passes from narrow, peg-like, elongated with parallel margins in anteriors to broadly rectangular, mesio-distally wide, labially short and with concave anterior margin in antero-laterals, to short and knob-like in postero-laterals. The lingual uvula is very short and further reduces from anterior to posterior positions. The tooth root vascularisation pattern is hemiaulacorhize in anteriors and antero-laterals, but holaulacorhize in postero-laterals.

In conclusion, even if our hypothetical taxon shows some similarities with the dentition of "*Xulagrodon*" (upright main cusp in anteriors, subequality between the height of the main cusp and the height of the lateral cusplets in postero-laterals, knob like labial crown apohysis on posterior teeth), many differences (median crest, labial and lingual ridges, reduced lateral cusplets, vascularization pattern of the root, in "*Xulagrodon*") preclude assignment to the same species. Nevertheless, the example of "*Xulagrodon*" lends further support for the hypothesised lumping of *Palaeobrachaelurus alisonae*, *Paleobrachaelurus* cf. *alisonae* and *Jurobatos cappettai* as described in the present paper.

An alternative proposition would consider an ontogenetic variation, with the morphotype *P.*

alisonae pertaining to mature individuals and the morphotype *P.* cf. *alisonae* to immature individuals, with *Jurobatos* attributed to posterior-most positions of *P.* cf. *alisonae*. This proposition is supported by the almost absence of the duo *P.* cf. *alisonae* + *Jurobatos cappettai* in Zoufftgen, when *P.* cf. *alisonae* is the dominant taxon of the Neoselachian fauna in Halanzy.

Occurrence - Couches à Crassum of Halanzy.

Palaeobrachaelurus vanessae n. sp.

Pl. 6

2010 Orectolobiforme gen. & sp. nov. – Delsate & Weis: pl. 6, fig. 10.

Type material - Holotype: MnhnL TM234 (Pl. 6 B, C). Dimensions of the holotype: mesio-distal length 1.4 mm. Paratypes: 3 teeth, MnhnL TM561 (Pl 6 A), MnhnL TM562 (Pl. 6 D, E), MnhnL TM564 (Pl. 6 G, H).

Additional material - 6 teeth from Dudelange-Zoufftgen, level 11 (in Delsate & Weis 2010).

Generic attribution - This material pertains to the genus *Palaeobrachaelurus* by its wing-like ("flügelartig") morphology, with a uvula and a more or less developed labial coronal apophysis, and its hemiaulacorhizy.

Derivatio nominis - Dedicated to Mme Vanessa Limpach (Musson, Belgium) for her long collaboration and assistance in my scientific research.

Locus typicus - Railway embankment, Dudelange-Zoufftgen, Luxembourg (Delsate & Weis 2010).

Stratum typicum - Toarcian, Marnes à *Astarte voltzi*, Level 11 (see Delsate & Weis 2010). Thouarsense Zone, Thouarsense and Bingmanni subzones.

Diagnosis - The crown is not ornamented; it bears a main cusp and 2 accessory cusplets on the expanded medial and distal wings. The basal apronal expansion of the crown does not produce a rectangular or rounded apophysis, but only a low convexity superimposed to the basal edge of the apron. This convexity is not very evident but is an important part of the diagnosis. The uvula is well developed, triangular with rounded tips, rather narrow (20 % of the total width of the crown), and perpendicular to the lingual base of the main cusp. The root is V-shaped, hemiaulacorhize. The species shows a well-marked monognathic heterodonty characterized by 1) the elongation of the mesio-distal width of the basal plate (less than the mesio-distal width of the crown on the anterior positions, equal on the lateral and posterior positions), 2) the increasingly marked distal inclination of the main cusp towards the commissure, and 3) the reduction of the mesial cusplet till its integration and near-disappearance in the cutting edge of the posterior and commissural positions, the conservation of the distal cusplet even in the posterior positions.

Description - The teeth measure 1 to 1.5 mm mesio-distally; the mesio-distal width of the holotype is 1.4 mm (paratype dimensions: see plates). The teeth are mesio-distally expanded, by mesial and distal wings (attribution to *Palaeobrachaelurus*), the crown is smooth, unornamented, with a clear but low labial protuberance of the apron; the triangular uvula is thin and short.

The crown bears one mesial and one distal accessory cusps on the anterior (paratype 1, TM561: Pl 6 A; TM563: 6 I; TM565: Pl. 6 J) and lateral (holotype, MnhnL TM234: Pl 6 B, C) positions, clearly separated from the main one on the anterior and lateral teeth, and followed by a free portion of the cutting edge to the lateral ends of the crown. Towards the back of the jaw, the mesial accessory cusp merges with the cutting edge (paratype 2, MnhnL TM562, Pl 6 D, E; paratype 3, MnhnL TM564, Pl 6 G, H); until the mesial cusp reduces or disappears with persistence of only the distal cusp on the postero-lateral positions (paratype 3, MnhnL TM564, Pl 6 G, H; TM568, Pl. 6 N).

The anterior positions (figs 6 A, 6 F, I and 6 J) have an elongated symmetrical crown with a slightly marked labial coronal apophysis. The crown bears a main cusp and 2 slightly diverging lateral cusplets that are about 1/3 of the height of the main one. The main cusp is straight on the anterior teeth. The mesial and distal expansions of the crown form cheeks laterally to the accessory cusps.

In the anterolateral and lateral positions (figs. 6 D, E, K, L, M, O), the mesio-distal width increases, the main and distal cusps incline distally, and the mesial one remains more upright. The main cusp is inclined distally at 70° on the holotype (lateral tooth). The apronal convexity is more marked because of the mesio-distal expansions of the crown,

The teeth of the postero-lateral positions (fig. 6 G, H, N) keep the apronal convexity, and the main cusp inclines progressively, with reduction of the crown height. The mesial accessory cusp reduces till being incorporated in the crown cutting edge, while the distal cusplet remains present under the inclined reduced main cusp. The main cusp is inclined distally at 60°-50° on the posterior teeth.

The basal plate of the holotype is damaged, but it is well preserved on paratypes 1 (MnhnL TM561), 3 (MnhnL TM564) and on MnhnL TM567 (Pl. 6 M). It is V-shaped, hemiaulacorhize with two lobes forming a 90° angle on the anterior positions and forming an obtuse V with stretched lobes on the posterior positions. In profile, the angle between the axis of the plane of the basal plate and that of the crown is very small.

Since such a morphology is not described for the "*Palaeobrachaelurus*-like" Orectolobiformes from the Toarcian to the Callovian, a new species is introduced for this form.

Discussion - The presence of a labial protuberance of the apron, even weakly marked, excludes the lateral positions of *Protospinax*, whose main cusp is also inclined, but not very high. The anterior positions of *Palaeobrachaelurus vanessae* is reminiscent of the anterior teeth of *Protospinax*. Nevertheless, *P. planus* Underwood, 2002 is excluded because it lacks lateral cusps, while *P. magnus* Underwood & Ward, 2004 has two pairs of short, rounded triangular lateral cusps differing from the accessory cusps of *P. vanessae*, which are hemicircle-shaped. Moreover the ratio {mesio-distal width / height} in *P. magnus* is 1.1 for an anterior tooth with two pairs of cusps (Underwood & Ward 2004) compared to 1.3-1.5 for anterior teeth of *P. vanessae* also with two pairs of cusps, (which are therefore more elongated). In addition, the lower edge of the crown of the anterior teeth of *Protospinax* is simply convex, without a labial protuberance of the apron.

Another difference pertains to functional wear. In fact, the apex of the main cusps of anterior teeth of *P. vanessae* is the preferentially abraded area (Pl. 6 A, J, L, N), while in *Protospinax*, generally all the cusps of the anterior teeth are abraded.

Furthermore, *P. vanessae* differs from some lateral or posterior positions of *Pseudorhina alifera* (Münster, 1842) by the presence of very well-developed lateral cusps (see Carvalho, Kriwet & Herzog 2008: fig.14 D, E and G; Thies & Leidner 2011) and the wing-like lateral expansions of *Pseudorhina alifera* that are thinner and not very high. In *Pseudorhina alifera* (Carvalho, Kriwet & Herzog 2008: fig 14, JME505 2210) the distal wing is reduced in width and height (without the cusp), the mesial wing remains long (without the cusp), the labial protuberance of the apron does not merge with the lower edge of the distal wing, and the basal plate is triangular with a central foramen. *P. vanessae* differs from the anterior teeth of *P. alifera* with lateral cusps in having a much shorter uvula and a different root (a central foramen on the triangular, cordiform basal plate, in *Pseudorhina*).

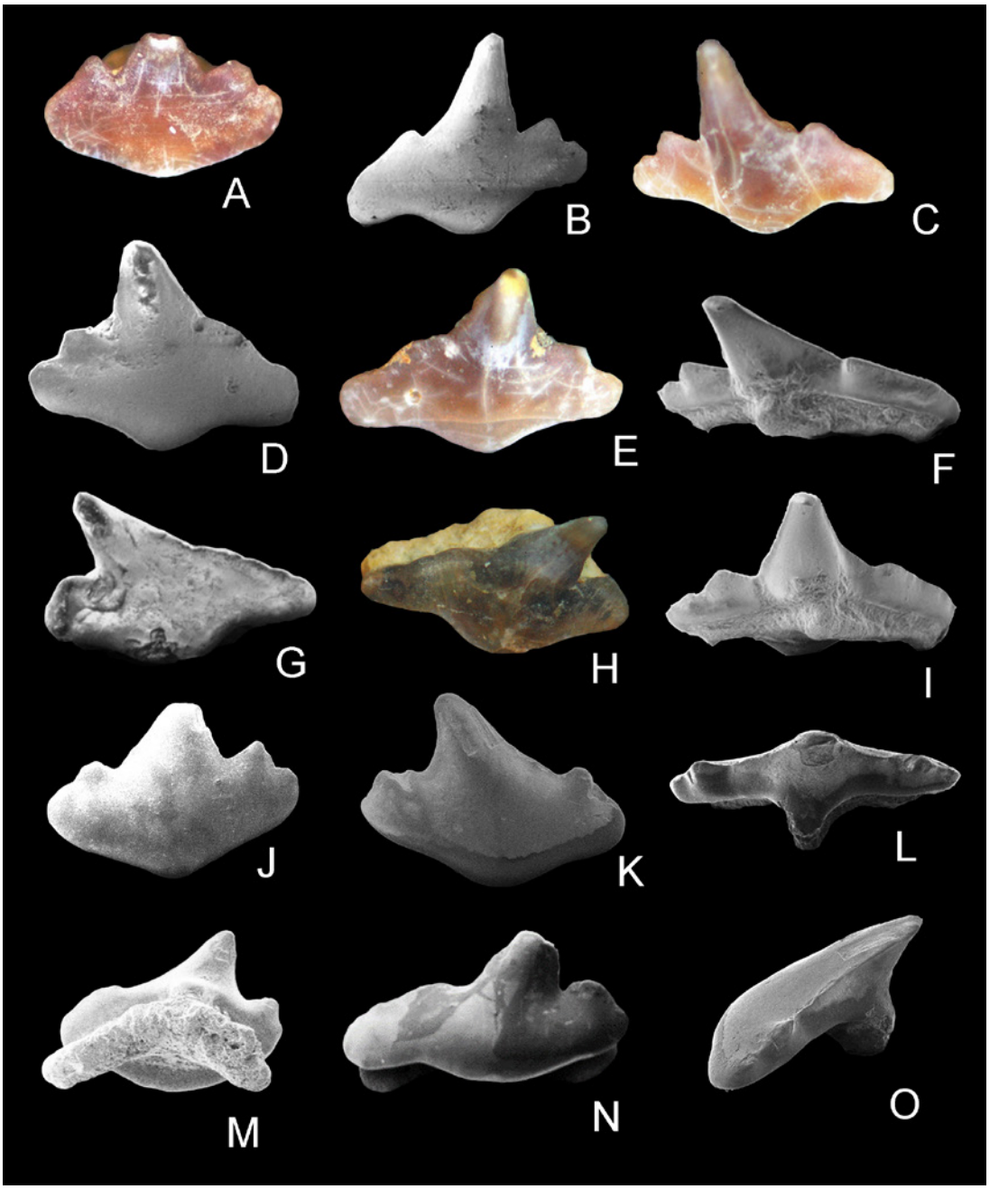
Teeth of *P. vanessae* and *Phorcynis catulina* Thiollière 1852 from the Kimmeridgian-Tithonian of Germany (see Thies & Leidner 2011) share the same pattern of low rounded apronal expansion of the crown and monognathic heterodonty, but they differ by the much wider expansion of the lateral wings in *P. vanessae* (the crowns of *Phorcynis* are narrower than crowns of *P. vanessae*), the width of the uvula of *Phorcynis* reaching 40% of the width of its narrower crown, a higher pointed and usually thinner main cusps in *Phorcynis catulina*, (BSPHG AS-1-1364) and in *Phorcynis sp.* (BSPHG 1960-XVIII-53 & 55), the absence of a proximal accessory cusp in *Phorcynis* sp. and *P. catulina,* very reduced to near-inexistent distal accessory cusps in *Phorcynis catulina* and presence of a low distal accessory cusp in *Phorcynis* sp.,and the presence of an ornamentation at the basal edge of the crown (short vertical ridges) in the lateral and posterior positions of *Phorcynis catulina* and *Phorcynis* sp.

In extant *Brachaelurus*, e.g. *Brachaelurus waddi* Bloch & Schneider 1801 (see Herman, Hovestadt-Euler & Hovestadt 1992), the posterolateral teeth possess a distally inclined main cusp, a reduced distal wing with disappearance of the distal cusp, but an elongated mesial wing with preservation of the mesial cusp.

The characteristics of the teeth of *Palaeobrachaelurus vanessae* (thin and short uvula, low apronal apophysis, the mesio-distal heterodontic variation

of the lateral cusps) are not observed in *P. alisonae*, *P. mussetti*, *P. aperizostus* and *P. bedfordensis*, nor in the Brachaeluridae or Hemiscylliidae, nor in the Orectolobiformes of the English Bathonian, i.e. *Dorsetoscyllium* and *Heterophorcynus* (Underwood & Ward 2004), which also differ from *P. vanessae* in the very high lower part of the crown.

In the postero-lateral positions of the Callovian *P. alisonae* (Thies 1983: pl. 10 fig. 5a) and *P. bedfordensis* (Thies 1983: Pl. 9 fig. 6a), the distal



cusp persists under the inclined main cusp, but the mesial cusp disappears while the mesial wing remains long. Moreover, the postero-lateral positions of *P. alisonae* and *P. bedfordensis* keep a stronger labial crown protuberance, instead of a simple superimposed convexity of the base of the crown in *P. vanessae*.

Palaeobrachaelurus vanessae furthermore differs from other species of genus in that the mesial wing undergoes a reduction in width and height, the mesial cusps merge with the mesial edge of the central cusp, forming a sharp edge, as soon as the antero-lateral positions (in *P. alisonae* and *P. bedfordensis*, this fusion only occurs from the posterior positions), the labial protuberance of the apron merges into the distal wing instead of remaining individualised in *P. alisonae*, *P. bedfordensis* and *Pseudorhina alifera* and the crown of the posterior teeth remains high, unlike those of *P. alisonae* and *P. bedfordensis*, which are then very low.

The number of lateral cusps of *P. vanessae* differs from *Palaeobrachaelurus bedfordensis* (on anteriors: 2 x 2 clearly individualized cusplets; on laterals: 2 mesial, 1 distal cusplets; on posteriors: 1 distal very low cusplet + 1 mesial blade-like ridge), and to a lesser extent from *P. aperizostus* (2 pairs of cusplets on anteriors > 2 x 1 cusplets + 2 x 1 marginal ear-shaped on laterals. The labial protuberance of the apron of *P. vanessae* is much less rectangular and less pronounced than in *P. bedfordensis*, less pronounced, less convex, or much less incised than in *P. aperizostus*, and lower and less tongue-shaped than in *P. alisonae*. The lingual section of the main cusp of *P. vanessae* is less convex than that of *Palaeobrachaelurus aperizostus* and *P. alisonae*. Finally, compared to *Palaeobrachaelurus mussetti* (Underwood & Ward 2004), which also shows two lateral cusps, the lateral wings of *P. vanessae* are more expanded, the basal part of the crown of *P. vanessae* is much lower, while it is strongly basally expanded and convex in *P. mussetti*, mostly in anterior positions, and incised in lateral positions, and the teeth of *P. vanessae* are larger (*P. mussetti* is small, less than 1 mm high).

Occurrence - *Palaeobrachaelurus vanessae* is abundant in Level 11 of Dudelange-Zoufftgen, (Thouarsense zone, Thouarsense and Bingmanni subzones) and in the Couches à Crassum of Halanzy. It is also present in the upper Toarcian of Feuguerolles (Calvados, F); the tooth GZB 1101 Delsate 2004: p. 43, Pl.3, Fig.1 from the Aalensis zone of Dudelange Ginzebierg and the specimen *Palaeobrachaelurus* BM693 from the Bajocian of Rumelange (L) (Delsate & Felten, 2015: p 23: fig 7 C Brachaeluridae indet. aff. *Palaeobrachaelurus* (MnhnL BM693). Vue labiale) are also posterior teeth of *P. vanessae*.

Orectolobiformes *incertae familiae*

Genus *Annea* Thies, 1983

Annea maubeugei Delsate & Thies, 1995

Pl. 7

1995 *Annea maubeugei* Delsate & Thies 1995.

2010 *Annea maubeugei* Delsate & Thies - Delsate & Weis: pl. 6, fig. 7.

2015 *Annea maubeugei* Delsate & Thies - Cappetta: p. 172, fig. 167.

Material - 1 tooth (Delsate & Weis 2010) from Dudelange-Zoufftgen (MnhnL TM231), level 11 (zone à Thouarsense, sous-zone à Thouarsense-Bingmanni), and 30 teeth from Halanzy (Couches à Crassum) including RBINS P62x (Pl 7 B, C), RBINS P6244 (Pl 7 D, E, F, H) and MnhnL TM569 (Pl 7 G).

Plate 6: *Palaeobrachaelurus vanessae* sp. nov. **A** - TM561, anterior tooth, paratype 1, mesio-distal width 1.0 mm; labial view; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **B-C** - TM234, lateral tooth, holotype; mesio-distal width 1.4 mm, labial view; 6 B is SEM mirror image of 6 C; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **D-E** - TM562, lateral tooth; paratype 2, mesio-distal width 1.3 mm, labial view; D is SEM mirror image of E; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni Subzones). **F, I** - TM563, anterior tooth, **F** - oblique lingual view, **I** - lingual view, mesio-distal width 1.46 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **G-H** - TM564, postero-lateral tooth, paratype 3, oblique labial view, mesio-distal width 1.5 mm; G is SEM mirror image of H; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **J** - TM565, anterior tooth, labial view, mesio-distal width 1.45 mm; Halanzy, Couches à Crassum. **K, L, O**: TM566, antero-lateral tooth, **K** - labial view, **L** - lingual-occlusal view, O: profile view, mesio-distal width 1.48 mm, crown height 0.97 mm; Halanzy, Couches à Crassum. **M** - TM567, antero-lateral tooth, basal view, mesio-distal width 1.1 mm; Halanzy, Couches à Crassum. **N** - TM568, postero-lateral tooth, labial view, mesio-distal width 1.8 mm; Halanzy, Couches à Crassum.

Description - *Annea* tooth characterized by a single vertical prominent crest of the labial face of the main cusp, of variable extension over the cusp and the apron (in *Annea carinata* Thies 1983, there are some additional divergent less marked folds).The crown bears only two lateral cusplets (one to two in *A. carinata*), of pyramidal shape in labial or lingual aspect (lateral cusplets much more slender and needle-like in *A. carinata*), with some ridges. The labial crown apophysis is well-marked and rounded rectangular. The uvula is long, flat, narrow, and tongue-shaped (it is more bulbous, bulky and rounded in *A. carinata*). The heterodonty of *A. maubeugei* is clearly figured and discussed in Delsate & Thies 1995. The root is hemiaulacorhize. The mesio-distal width of MnhnL TM231 is 0.8 mm.

Occurrence - *Annea maubeugei* is present in Halanzy, Couches à Crassum and in level 11, at Dudelange-Zoufftgen (Thouarsense Zone, Thouarsense and Bingmanni subzones), it is furthermore present in the Serpentinum Zone at Feuguerolles (Calvados, F).

Genus *Ornatoscyllium* Underwood & Ward, 2004

Ornatoscyllium cf. *pattersoni* (Thies, 1983)

Pl. 8

2010 *Ornatoscyllium* sp. - Delsate & Weis: pl. 6, fig. 8.

Material - 5 teeth from level 11 of Dudelange-Zoufftgen (including MnhnL TM232, TM570), 10 teeth from Halanzy (Couches à Crassum (not reported by Delsate *et al* 1989, nor Delsate & Lepage 1990, although present in the Couches à Crassum from Halanzy) including MnhnL TM571.

Description - A vertically folded form, with three vertical folds reaching almost the apex of the main cusp, and bearing a node at their base, in addition to each pair of lateral cusps bearing three folds, reminiscent of *Orectoloboides* from the Cretaceous and close to *Ornatoscyllium (Orectoloboides) pattersoni* (Thies, 1983) from the Callovian and Bathonian of England (Underwood & Ward 2004).

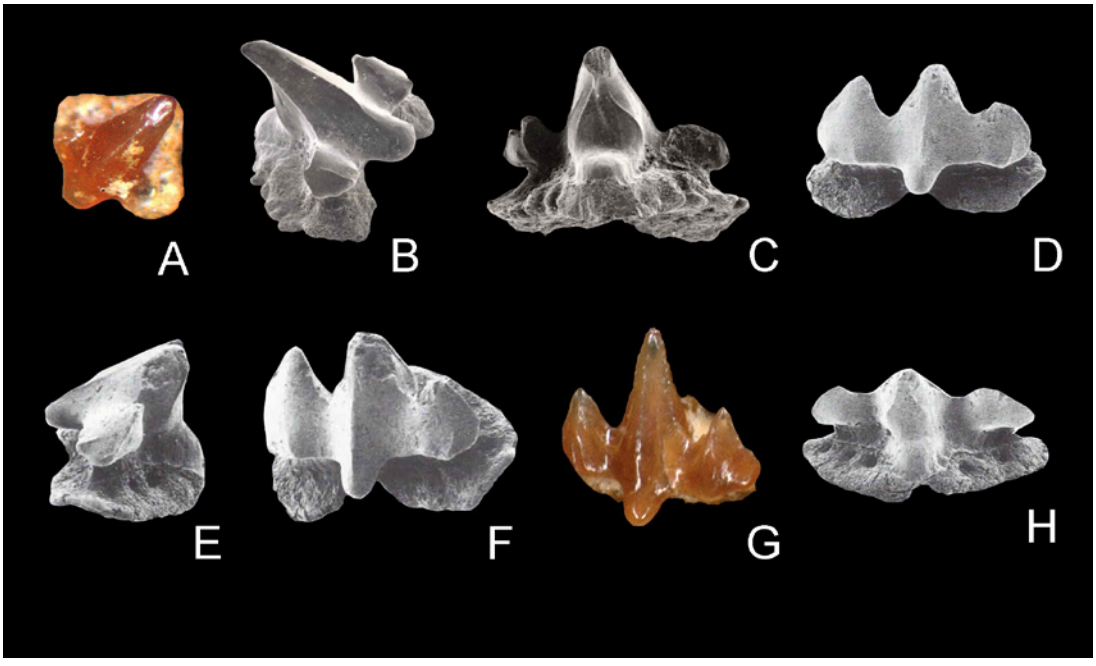


Plate 7: *Annea maubeugei* Delsate & Thies 1995. **A** - TM231, antero-lateral tooth, labial view, mesio-distal width 0.75 mm: Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **B-H** - Halanzy, Couches à Crassum. B, **C** - RBINS P62x, anterior tooth, **B** - oblique labial profile, **C** - lingual view, mesio-distal width: 0.89 mm. D, E, F, **H** - RBINS P6244, lateral tooth, paratype 6, **D** - labial view, **E** - profile, F., labial oblique view, H. lingual view, mesio-distal width: 0.59 mm, crown height from apex to apron: 0.36 mm. **G** - TM569, anterior tooth, labial view, lingual view, mesio-distal width: 0.95 mm, height of the crown from apronal apophysis to apex of the central cusp: 0.90 mm.

The differential diagnosis with *Ornatoscyllium freemani* Underwood & Ward, 2004 from the Bathonian of England is based on the ornamentation of vertical folds already abundant on the anterior positions of *O. pattersoni*, while the crown of the anterior positions of *O. freemani* are nearly free of ridges except one single high ridge reaching the labial protuberance at the base of the crown. The Zoufftgen specimen is an anterior tooth with many vertical folds, while the Halanzy Crassum specimen is an anterolateral position, ornamented by many segments, stronger and more abundant at the base of the crown. The posterior teeth of both species are very similar and ornamented by short strong vertical ridges. The mesio-distal width of TM232 is 1 mm.

Occurrence - Dudelange-Zoufftgen level 11 (Thouarsense zone, Thouarsense and Bingmanni subzones); Halanzy (Couches à Crassum); the Serpentinum Zone of Tolgyhat (Mounts Gerecse, Hungaria); the Callovian of Rookery Pit (England), Thies 1983, 108 Pl 11: figs 1-4.

Family Hemiscylliidae Gill 1962

Remarks - We consider the new genera *Eoscyllium* and *Thiesocyllium* as well as *Pseudospinax* Muller & Didrich, 1991 (see Underwood 2002: 304-305), to be included into Hemiscylliidae, or a not yet described orectolobiform family, rather than Brachaeluridae, on the basis of the cusp and cusplet pattern and relationships and the absence of expanded mesio-distal wings bearing cusplets clearly separated from the main cusp. This is rather evident in extant Orectolobiforms (see Herman *et al* 1992) and seems to be an economic hypothesis, pending evidence proving the opposite.

Genus *Eoscyllium* nov. gen.

Type species - *Heterodontus duffini* Thies, 1983 (here designated).

Derivatio nominis - eo: greek in the sense of "early", *Scyllium* because of the typical Hemiscylliidae morphology similar to taxa as *Chiloscyllium*

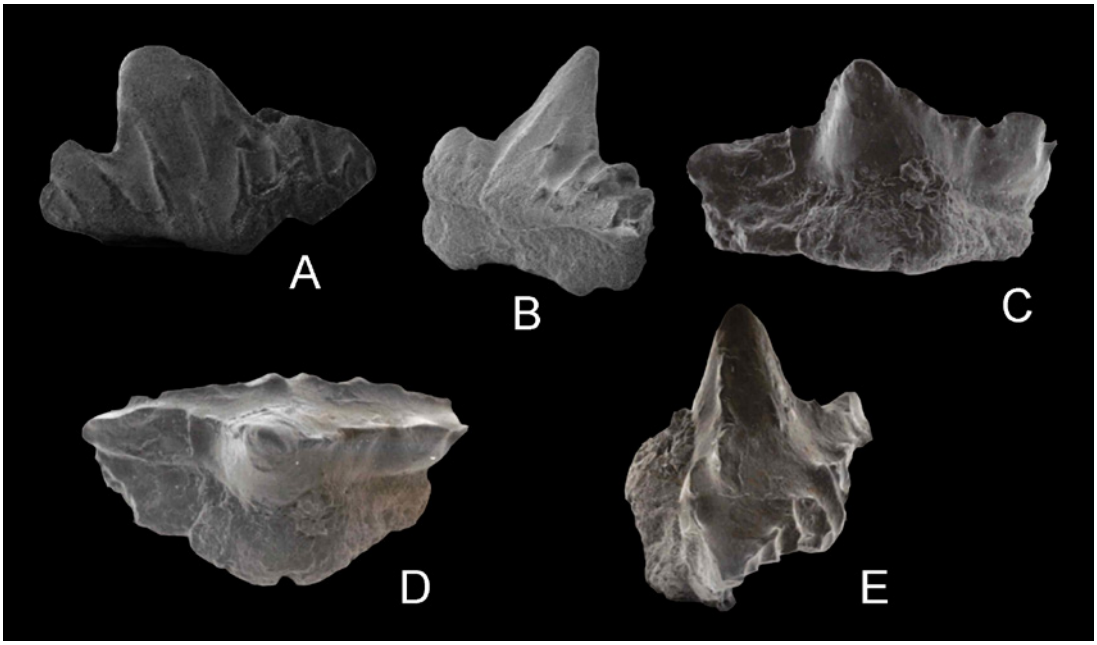


Plate 8: *Ornatoscyllium* cf. *pattersoni* (Thies 1983). A - TM232, labial view; mesio-distal width 1.0 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). B - TM241, labial oblique view, mesio-distal width 0.9 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). C-E - TM571, C - lingual view, D - apical view, E - labial profile, mesio-distal width 0.9 mm; Halanzy, Couches à Crassum

plagiosum (see Herman *et al* 1992: pl. 9) and *Hemiscyllium* sp Underwood & Mitchell 1999: p. 19 & pl. 4, figs. 10-12.

Generic diagnosis - As for the type species**.**

Eoscyllium duffini (Thies, 1983)

Pl. 9

1983 *Heterodontus duffini* nov. sp. - Thies 1983: pl. 6, fig. 4 and pl. 7, figs. 1-8.

1989 *Squalogaleus* - Delsate, Herman & Lepage 1989: pl. 1, fig. 3.

1989 *Chiloscyllium* sp - Delsate, Herman & Lepage: pl. 1, fig 5.

1990 (*Squalogaleus*?) lingual occlusal view - Delsate & Lepage: fig. 3A.

1990 Hemiscylliidae cfr *Chiloscyllium* (labial view) - Delsate & Lepage: fig 4.

2002 Gen. and sp. indet. – Underwood: pl. 1, fig. 12 (Kimmeridgian).

2004 Galeid indet P66044 - Underwood & Ward: pl. 1, fig. 5 (Bathonian).

Holotype - *Heterodontus duffini* SMF 7117 from Moorberg (D) upper Toarcian and upper Aalenian (Thies 1983 fig 4 a-c).

Other Material - 19 teeth including MnhnL TM 233, TM 572 (Zoufftgen)**;** 30 teeth including MnhnL TM574, TM575, TM576, TM577, TM578 (Halanzy).

Diagnosis - The crown lacks any ornamentation. Those of the anterior positions are highly symmetrical. The crown bears 3 cusps: a high and slender main cusp (upright on anterior positions, distally inclined on lateral positions) and 2 low accessory cusplets, one mesial, one distal, equalling 15-25 % (anterior positions) of the main cusp height.

The basal part of the crown (about 40 % of the total crown height) overhangs the root by an apron, perfectly rounded (anterior position) or slightly oval (lateral positions). There is no labial apophyse developed on the basal edge of the crown. The uvula is nearly perpendicular to the lingual face of the main cusp; it is rather short (half the height of the lingual surface of the root). The mesio-distal width is about 0.5-0.6 mm (measured on supposed juvenile teeth) (Thies 1983: 28) and does not increase in posterior positions. The monognathic heterodonty sees the progressive inclination of the main cusp, with the lowering of the 2 accessory cusps, the mesial one becoming very low. The 2 accessory cusps disappear on the commissural positions, fused in the crown profile. The root is V shaped and rather high. A central foramen is open in the 90 ° angle between the 2 root lobes, and a medio-internal foramen opens under the uvula.

Description - The juvenile teeth have a mesio-distal width of 0.4 mm to 0.6 mm; their height is 0.35 mm to 0.6 mm; the mesio-distal width of the adult teeth is perimillimetric. In all teeth, the root is V-shaped (hemiaulacorhize) with wings diverging by at least 90°. The basal surface of the root has a central foramen in the angle of the lobes. The base of its lingual surface has a medio-internal foramen. The crown is unornamented and smooth. It is not very expanded mesio-distally, i.e. there is no mesial nor distal wings bearing the accessory cusps. It has a main cusp and 2 small accessory cusplets not exceeding a quarter of the height of the main cusp and clearly separated from the main cusp by a well-marked incision. The labial edge of the crown is convex, it hides the labial surface of the root, forming a semicircular apron, without marked development of a labial crown protuberance. The uvula is triangular with a rounded apex and can extend up to half the height of the lingual surface of the root. The crown of the antero-mesial teeth is symmetrical. It has a high and straight main cusp and two small accessory cusps of which the axis diverges from that of the main cusp, from the front and from the profile.

Regarding the heterodontic gradient from symphyseal positions to posterior positions, the height of the labial edge of the crown reduces, implying that its perfectly hemi-circular outline in anterior teeth passes gradually to an oval outline. The main cusp of the anterior teeth is slender and vertical, it inclines distally with decreasing height in commissural direction (the crown of the lateral teeth is asymmetrical), while the accessory cusps, also inclined distally, gradually merge with the cutting edge of the crown till the near-disappearance of the mesial accessory cusp, while the distal accessory cusplet remains present in posterior positions.

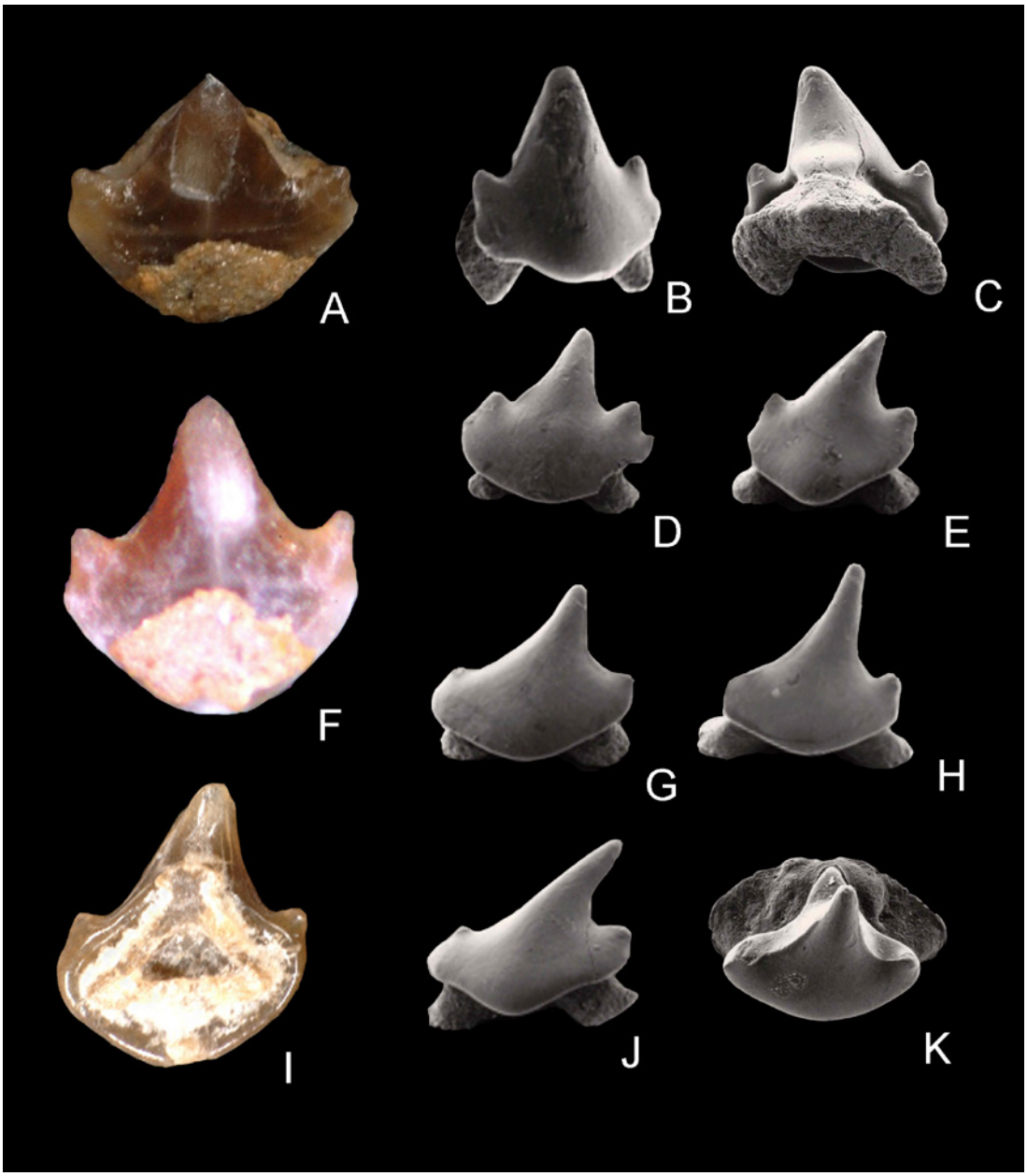


Plate 9: *Eoscyllium duffini* (Thies, 1983) and *Eoscyllium* aff. *Duffini* (Thies, 1983). **A, F** - TM233, *Eoscyllium duffini* (Thies, 1983), anterior tooth, 2 labial views, mesio-distal width 1.1m; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **B, C** - TM573, *Eoscyllium* aff *duffini* (Thies, 1983), **B** - labial view; **C** - lingual view, mesio-distal width 1 mm; Couches à Crassum, Halanzy. **D** - TM574, *Eoscyllium duffini* (Thies, 1983), labial view; mesio-distal width 0.85 mm; Couches à Crassum, Halanzy. **E** - TM575, *Eoscyllium duffini* (Thies, 1983), labial view; mesio-distal width 0.80 mm; Couches à Crassum, Halanzy. **G** - TM576, *Eoscyllium duffini* (Thies, 1983), labial view; mesio-distal width 0.70 mm; Couches à Crassum, Halanzy. **H, K** - TM577, *Eoscyllium duffini* (Thies, 1983), **H** - labial view, **K** - apical view, mesio-distal width 0.80 mm; Couches à Crassum, Halanzy. **I** - TM572, *Eoscyllium duffini* (Thies, 1983), anterior tooth, basal view of the crown, mesio-distal width 1 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **J** - TM578, *Eoscyllium duffini* (Thies, 1983), labial view; mesio-distal width 0.85 mm; Couches à Crassum, Halanzy.

Discussion - Thies (1983) attributed this species to juveniles of Heterodontiformes (Thies 1983: 28-30), occupying a different niche from the adults with larger and possibly heterodontic dentition (molariforms in larger individuals). Either way, we would rather expect higher and more subequal cusps and more asymmetrical crowns, or higher and more numerous accessory cusps, for a heterodontiform attribution. The morphology of *Eoscyllium (Heterodontus) duffini* is more evocative of *Chiloscyllium* or *Hemiscyllium*.

The teeth of *Eoscyllium duffini* (Thies 1983) figured and described (Pl. 6, fig. 4 and Pl. 7, figs. 1-8) by Thies (1983) from the Upper Toarcian of Moorberg are similar to this material from Dudelange-Zoufftgen (Thouarsense Zone) and Halanzy (Couches à Crassum). In agreement with Underwood (2002: 306), we attribute the teeth of *Eoscyllium* (*Heterodontus*) *duffini* to an Orectolobiform. This morphology is reminiscent of the orectolobiforms Hemiscylliidae, excluding the orectolobiform *Palaeobrachaelurus* (*P. alisonae, P. aperizostus, P. bedfordensis, P. vanessae* sp. nov.) because of the absence of mesio-distally very expanded wings of the crown and of a marked labial apronal protuberance in *E. duffini*. Nevertheless, *E. duffini* shows some resemblance with *Palaeobrachaelurus mussetti* Underwood & Ward, 2004 but, even if the labio-basal part of the anterior tooth is rounded, more lateral teeth of *P. mussetti*, show a concave indentation (absent in *E. duffini*). Moreover, the lower part of the crown of *Eoscyllium* is much shorter and its uvula is narrower, better differentiated and triangular.

The great height of the main cusp relative to that of the lateral cusps precludes assignment to the heterodontiform *Paracestracion*, showing subequal cusps, and the Protospinacidae *Protospinax*, never showing a very high main cusp even if the latter is well marked on the anterior teeth.

The clear incision between the cusps of *Eoscyllium duffini* sets aside the anterior positions of *Protospinax*, of which the cusps are not separated by deep incisions.

The Hemiscylliidae *Pseudospinax muftius* (Thies, 1983) differs from *Eoscyllium* (*Heterodontus*) *duffini* by a basal edge of the crown that is more elongated and the tongue-shape instead of perfectly hemicircular or round oval as in *Eoscyllium duffini* (Underwood & Mitchell 1999). Anyway, *Pseudospinax muftius* shows some similarities with *Eoscyllium duffini*, as evidenced by the specimens of *P. muftius* Thies (1983): pl. 5 figs 1.2 and pl. 6 figs 1.2.3. that are very similar to *Eoscyllium duffini*, pl. 7, figs 1-8. The morphotypes of the 2 taxa show striking similarities, for example the heterodonty, the inclination of the main cusp on the axis of the crown, and the strong and long uvula, except that *P. muftius* is two times larger than *E. duffini*.

The orectolobiform *Heterophorcynus* Underwood & Ward (2004) has an even higher crown than *P. mussetti,* one to two pairs of lateral cusps and a very massive root. *Dorsetoscyllium* Underwood & Ward (2004) has no lateral cusps and a very wide main cusp.

In *Pseudorhina alifera*, the uvula is clearly longer, as opposed to short and triangular in *Eoscyllium*, the labial protuberance of the apron is very clearly marked, and the root is triangular with a central foramen.

Several teeth from Halanzy as well as teeth from Zoufftgen bear 2 tiny marginal protrusions (not really cusplets) of the crown under the base of the 2 accessory cusps, with a slightly deeper apron; this character is also present in *Hemiscyllium* sp. (Underwood & Mitchell 1999) and could be the result of heterodontic variation of *Eoscyllium duffini*, or indicate the presence of another species of *Eoscyllium* close to *duffini*. I refer such a tooth (TM573) to *Eoscyllium* aff. *duffini* (Pl. 9 B, C)

Occurrence - Couches à Crassum of Halanzy (B), Saint-Mard (B), Longlaville (Longwy, F), Ludres (Nancy, F); the Grand Duchy of Luxembourg: Couches à Crassum: Level 4 (Bifrons zone, Bifrons subzone) and 5 (Variabilis zone, Illustris and Variabilis subzones) up to Level 11 (Thouarsense zone, Thouarsense and Bingmanni subzones) of Dudelange-Zoufftgen, the Couches à Crassum at Belvaux (L); the Upper Toarcian of Germany: Moorberg (Hannover): (Thies 1983), Dispansum to Aalensis zone to Upper Aalenian (Scissum and Murchisonae zone); the Bathonian and Kimmeridgian of England.

Genus *Thiesoscyllium* nov. gen.

Type species - *Thiesoscyllium underwoodi* sp. nov.

Derivatio nominis - A tribute to the palaeo-ichthyologist Detlev Thies (Hannover) for his lifelong

contributions to the knowledge of Chondrichthyans, their anatomy, their dentition and squamation, and his pristine anatomical descriptions of Actinopterygian anatomy and dentition. The suffix *-scyllium* for the morphology of the teeth here described, very close to the orectolobiforms (carpet sharks) and hemiscylliidae (bamboo sharks).

Generic diagnosis - The teeth feature a lozenge-shaped crown: a deep and wide rounded basal part of the crown bears a large and wide main cusp; the lateral corners of the lozenge are not expanded in mesio-distal wings, each lateral cutting edge bears one tiny or faint accessory cusplet, about 1/8 of the height of the main cusp. The basal part of the crown (apron overhanging the root) does not produce a labial apophysis. The lingual base of the main cusp produces a nearly perpendicular uvula, wide and long. The root is V-shaped, hemiaulacorhize.

Remarks - The teeth here assigned to the new genus *Thiesoscyllium* can be distinguished from *Palaeobrachaelurus* and members of the Brachaeluridae by the less developed expansion of the lateral crown corners.

Thiesoscyllium underwoodi sp. nov.

Pl. 10

Material - 11 teeth from Halanzy, Couches à Crassum.

Derivatio nominis - Species dedicated to Charlie Underwood in honour of his works on Jurassic and Cretaceous chondrichthyan faunas and the evolution and development of fishes.

Locus typicus - Halanzy (B), rue des Vergers.

Stratum typicum - Toarcian, "couches à Crassum ".

Holotype - MnhnL TM580 (Pl. 10 B). Dimensions of the holotype: the mesio-distal width is 1.5 mm, the total height is 1.5 mm, 50 % of which are the main cusp.

Paratypes - paratype 1, mesio-distal width 1.2 mm (MnhnL TM579: Pl. 10 Fig. A, D, F); paratype 2, mesio-distal width 1.1 mm (MnhnL TM581: Pl. 10 C), and paratype 3, labio-lingual length 0.75 mm (MnhnL TM582: Pl 10 E).

Diagnosis and description - The species based on isolated teeth, of 1 to 1.5 mm mesio-distal width. The holotype illustrates the specific description. The crown of *Thiesoscyllium underwoodi* is lozenge-shaped, with very slightly expanded mesio-distal wings, the crown base is a V-shaped apron, not rounded, nor convex with incision, it does not produce any labial coronal apophysis. Its accessory cusplets show some damage at their junction with the main cusp. The apex of the main cusp is broken or worn. The lateral cusplets of paratype 1 are intact, the apex of the main cusp is also broken. The 3 cusps of paratype 2 are obliquely truncated, which gives an idea of the functional wear of these teeth. Paratypes 2, 3 and 4 show the rounded triangular uvula: its base equals 25 % of the mesio-distal width of the tooth, and it extends to 50-75% of the height of the root. The paratypes provide details of the root, which is V-shaped and hemiaulacorhize. The basal face of root lobes bears about 5 foramina each. A central foramen is situated at the labial angle between the 2 lobes of the root, a medio-external foramen is present at the lingual angle of the root, the external face of each root lobe bearing a larger foramen.

Discussion - The deeper development of the apron (basal part of the crown overhanging the root) of *Thiesoscyllium underwoodi* distinguishes it from *Protospinax*, as well as from *Pseudospinax* (Müller & Diedrich, 1991; Underwood & Mitchell, 1999; Underwood 2004; Kriwet, 2003), of which the main cusp is narrower, more acuminate, and lower in structure. *Thiesoscyllium underwoodi* is reminiscent of *Pseudorhina alifera* and *Pseudorhina* sp. (see Thies & Leidner 2011), but these are more cross-shaped than lozenge-shaped, their main cusp is narrower, they develop a deeper rectangular or rounded labial apophysis of their apron, and they have more developed lateral expansions. In addition, *Pseudorhina* sp. and some teeth of *Pseudorhina alifera* do not bear any accessory cusp, other teeth of *Pseudorhina alifera* bear two accessory cusps on their expanded wings. *Palaeobrachaelurus* sp. 1 (Thies 1989: fig. 2a,b) from the Upper Aalenian of Germany differs from *Thiesoscyllium underwoodi* by its cross shaped (not lozenge-shaped) crown pattern, with a large labial tongue-shaped crown apophyse (not a V-shaped apron like in *Thiesoscyllium*), the wider expansion of the lateral wings of its crown, and the taller and diverging lateral accessory cusps (1 pair

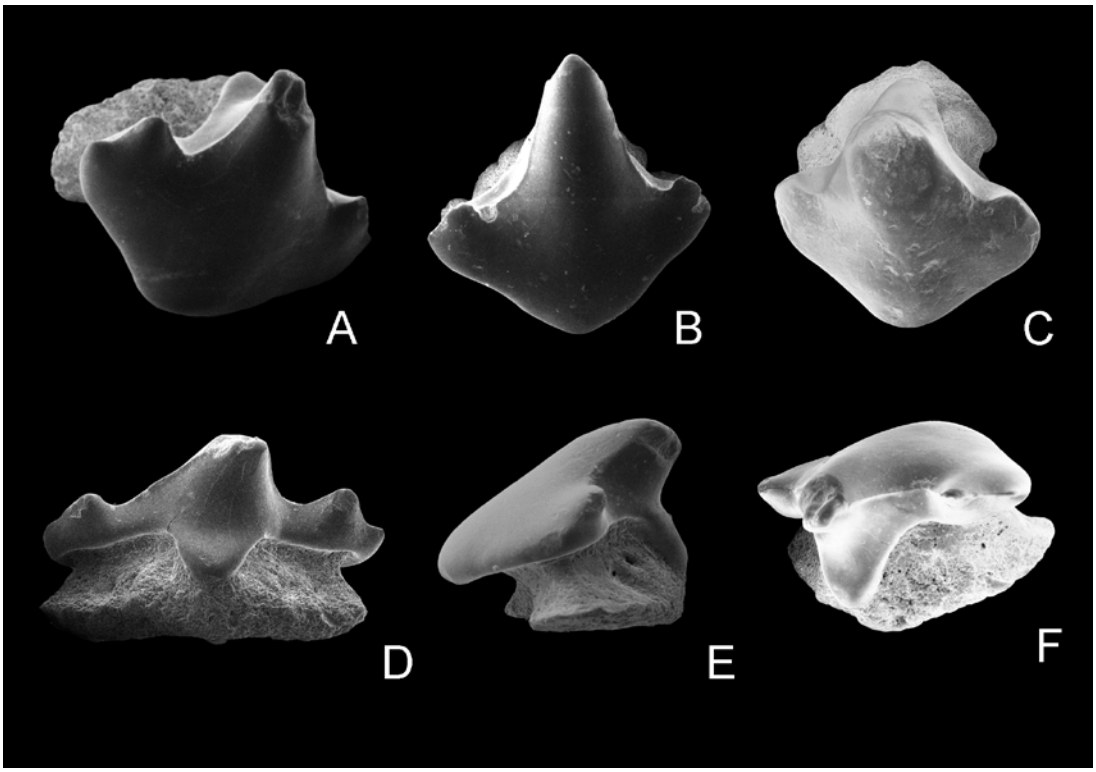


Plate 10: *Thiesoscyllium underwoodi* nov. gen., n. sp. A, D, F - TM579, paratype 1, A - labial oblique view, D - lingual view, F - lingual oblique view, mesio-distal width 1.2 mm; Halanzy, Couches à Crassum. B - TM580, Holotype, labial view, total mesio-distal width 1.5 mm, total height 1.5 mm; Halanzy, Couches à Crassum. C - TM581, paratype 2, occluso-labial view, mesio-distal width 1.1 mm: Halanzy, Couches à Crassum. E. TM582, paratype 3, profile, labio-lingual length 0.75 mm; Halanzy, Couches à Crassum.

+ 1 pair of faint cusplets). *Mesiteia*? sp (Thies 1989: fig 11a,b,c) from the Upper Bajocian of Germany differs from *Thiesoscyllium underwoodi* by its cross shaped (not lozenge-shaped) crown pattern, with a narrower crown and main cusp, 2 hook like accessory cusps, and a very deep and wide labial crown tongue-shaped apophyse (not a V-shaped apron like in *Thiesoscyllium*).

Thiesoscyllium underwoodi is reminiscent of *Palaeobrachaelurus mussetti* (Underwood & Ward 2004), which also has two lateral cusps. The latter, however, are more hook like, and the basal part of the crown of *P. mussetti* is strongly expanded and convex in anterior positions and incised in lateral positions. In addition, *Palaeobrachaelurus mussetti* is smaller, less than 1 mm high. The characteristics of the teeth of *Thiesoscyllium underwoodi* from Halanzy (narrow uvula, rounded lozenge labial face, very slightly expanded wings) are not observed in *P. alisonae*, *P. aperizostus* and *P. bedfordensis*, nor in the Brachaeluridae nor in the Orectolobiformes of the English Bathonian, i.e., *Dorsetoscyllium* and *Heterophorcynus* (Underwood & Ward 2004), which both have a very high lower crown.

Because of the absence of expanded mesio-distal wings, the specimens described above cannot be assigned to the genus *Palaeobrachaelurus* which is characterised by its "flügelartige" morphology, with uvula and more or less developed apron, and its hemiaulacorhizy, neither to other members of the Brachaeluridae. Instead, they are assigned to the Hemiscyllidae or to a not yet described orectolobiform family.

Thiesoscyllium underwoodi furthermore differs from the Bajocian aff. *Palaeobrachaelurus mussetti* Underwood & Ward, 2004 (plate 7 fig D to H, in

Delsate & Felten 2015 (MnhnL BM655, BM657, BM656, BM658 & BM393-RUMA06) on account of its better differentiated lateral cusplets, its more slender and narrower uvula (base 25 % of the mesio-distal width of the tooth), and the less developed basal part of its apron. This latter material is hereunder attributed to *Thiesoscyllium felteni*, nov. gen. nov. sp., also consisting of millimeter-sized, lozenge-shaped teeth bearing a high main cusp flanked by two lateral cusps.

Remark - The Bajocian teeth attributed to aff. *Palaeobrachaelurus mussetti* by Delsate & Felten (2015) are attributable to this new genus on account of their lozenge-shaped crown, their low accessory cusps, and the absence of a labial apophysis of the crown.

Occurrence - Couches à Crassum of Halanzy (B).

Thiesoscyllium felteni sp. nov.

2015 aff. *Palaeobrachaelurus mussetti* Underwood & Ward, 2004 - Delsate & Felten, pl. 7 fig. D-H.

Derivatio nominis - Named in honour of Roland Felten (Dudelange) in recognition of its meticulous exploration of the Luxembourg Bajocian sediments.

Holotype – MnhnL BM655, figured in Delsate & Felten 2015, pl. 7 fig. D.

Paratypes – 4 paratypes MnhnL BM656, BM657, BM658, BM393, figured in Delsate & Felten 2015, pl. 7, figs, F-H.

Locus typicus - Ottange-Rumelange stone quarry, Luxembourg.

Stratigraphy – Marnes d'Audun-le-Tiche member, lower Bajocian, Humphresianum Zone.

Description - The species differs from its only known congener *T. underwoodi* in a wider uvula (its base reaching 45 % of the mesio-distal width of the tooth), less developed accessory cusplets, a deeper basal part of the crown (apron), and a low keel developed from the top of the labial face of the main cusp to its base.

Occurrence - Lower Bajocian of Ottange-Rumelange (Luxembourg).

Galeomorphi indet
? Orectolobiforms

Genus *Jurobatos* Thies, 1983

Jurobatos cappettai Thies, 1983
Pl. 11

1993 *Jurobatos cappettai* - Thies 1993.

2012 *Jurobatos cappettai* - Cappetta: 324-325.

Material - 1 tooth from the top of the Bifrons Zone of Zoufftgen (non reported by Delsate & Weis 2010), 70 teeth from the Couches à Crassum of Halanzy, including MnhnL TM583, TM584, TM585.

Description - The mesio-distal width is around 1 mm. The crown shows strongly expanded lateral heels there are three low cusps, with a blunt main cusp. The main cusp may be slightly distally inclined, but the accessory cusps show very little asymmetry There is often a knob on the lingual face of the crown above the vestigial uvula. The labial coronal apophysis is of variable development among the specimens. The surface of the crown is usually smooth, but some specimens show variable vertical folds on the lingual face of the main cusp over the "knob" and also on the lingual face of the lateral cusps, as well as on the labial face. The roots have the shape of an elongated bar, they show two vascularization patterns: hemiaulacorhize with a central labial foramen and a medio-lingual foramen, or holaulacorhize with a central foramen.

Remarks - The Toarcian specimens from Germany were first described as batoids (Thies 1992). Thies (1993) then provided data from the new material of Halanzy (Couches à Crassum) in particular the presence of a parallel-fibred enamaloid, which is an autapomorphy of the Neoselachians, prompting the recognition of *Jurobatos* as a galeomorph shark instead of a batoid (Thies, 1993). These low teeth with 3 cusps and a labial protuberance show some similarities with the lateral positions of *Annea* but differ by a less marked apron and low cusps while *Annea* keeps relatively high and well separated cusps and cusplets on the posterolateral positions (see Delsate & Thies 1995), and a strong uvula. Furthermore, there are similarities with the lateral positions of *Palaeobrachaelurus* (see Thies 1983), but these show inclined main cusps remaining relatively high, and a well-developed uvula. Nevertheless, see the discussion

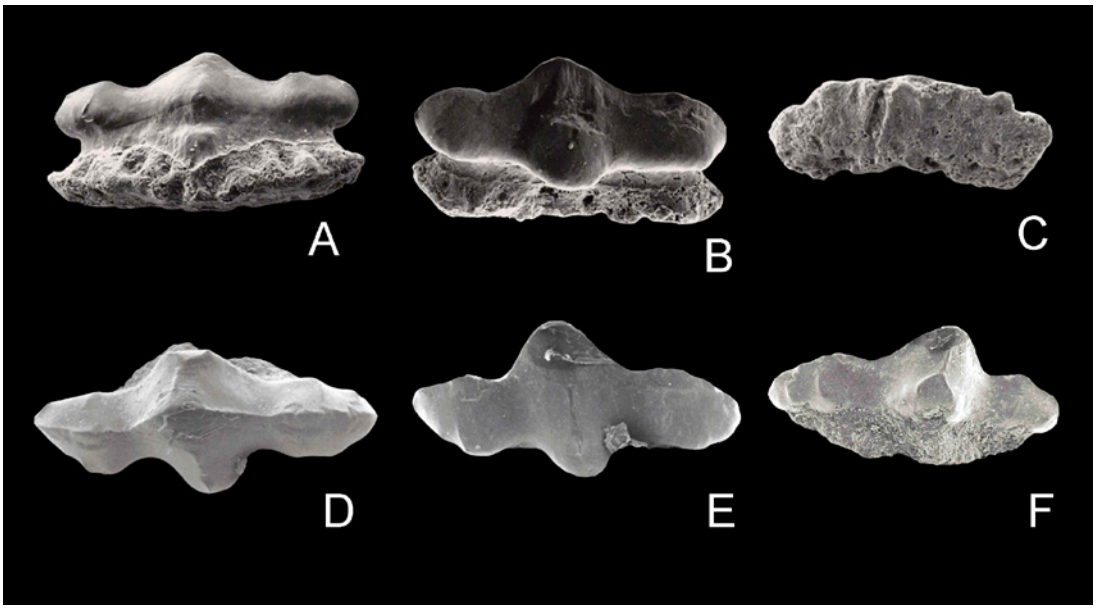


Plate 11: *Jurobatos cappettai* Thies, 1983. A, C - TM583, A - lingual view, C - oblique basal view, mesio-distal width 0.66 mm; Halanzy, Couches à Crassum. B - TM584, labial view, mesio-distal width 0.64 mm; Halanzy, Couches à Crassum. D, E, F - TM585, D - occlusal view, E - labial view, F - lingual view, mesio-distal width 0.95 mm; Halanzy, Couches à Crassum.

about the hypothesized gathering of *Palaeobrachaelurus alisonae*, *Palaeobrachaelurus* cfr *alisonae* and *Jurobatos cappettai*, in the "*alisonae*" chapters.

Occurrence - Upper Toarcian of Germany, Moorberg (Hannover), Couches à Crassum of Halanzy (Thies 1993) and Lorraine; level 4, (Bifrons Zone, Bifrons Subzone) of Dudelange-Zoufftgen.

Note about Orectolobiformes and Squatinomorphs

The Orectolobiforms are common in Dudelange-Zoufftgen, especially in level 11 (Thouarsense zone, Thouarsense and Bingmanni subzones). It should be noted that it is very difficult to precisely identify isolated orectolobiform-type teeth, as the morphologies are plesiomorphic, and differentiation from Squatiniformes is not easy. Thus, the study of complete specimens of Squatiniformes (Carvalho *et al* 2008) has allowed to rehabilitate *Pseudorhina alifera* and *P. acanthoderma* and to establish the distinctive characteristics of their teeth. Certain positions of *Pseudorhina alifera* (Leidner & Thies 1999; Carvalho *et al* 2008) are similar to teeth from Dudelange-Zoufftgen or Halanzy that we tend to consider as part of the variation of Galeomorphii Orectolobiformes reminiscent of *Palaeobrachaelurus* or *Eoscyllium (Heterodontus) duffini* Thies, 1983 (see above). Likewise, the teeth of juvenile specimens of *Pseudorhina alifera* are reminiscent of *Eoscyllium duffini* Thies, 1983 (see above) and *Mesiteia*. The teeth of juveniles have two lateral cusps, absent in adults. On the postero-lateral teeth, the main cusp remains straight, barely inclined, while reducing. The lateral wings of the teeth of *P. alifera* are thin and elongated. Orectolobiforms and *Pseudorhina* share a well-marked labial protuberance of the apron. Two characteristics distinguishing the teeth of *Pseudorhina* from those of Orectolobiforms are the isolated central foramen on the triangular basal plate, and the long and powerful uvula.

Super Order Squalomorphi
Order Squatiniformes Buen 1926
Family Squatinidae Bonaparte, 1838

Genus *Pseudorhina* Jaekel 1898

Pseudorhina alifera (Münster, 1842)
Pl. 12 A, B

Material - 1 tooth from Zoufftgen (Mnhnl TM586).

Description - This is a narrow anterior tooth with a very high main cusp, short mesial and distal wings, no lateral cusp, and an isolated central foramen on the basal plate. It is similar to the specimens of *Squatina frequens* from the Kimmeridgian (Underwood, 2002: Pl. 4, figs. 3 to 8, P.65698 and P.65699) or *Pseudorhina alifera* (Münster, 1842), see fig. 14b (PIMUZ AII 3050) described by Carvalho et al. (2008) from the Upper Jurassic.

Occurrence - Level 11 of Dudelange-Zoufftgen (zone at Thouarsense, sub-zones at Thouarsense and Bingmanni); Kimmeridgian to Tithonian of Germany (Cappetta 2012).

Pseudorhina acanthoderma (Fraas, 1854)

Pl. 12 C, D

Material - 1 tooth from the locality Halanzy (Couches à Crassum) (MnhnL TM587).

Description - see the paragraph "Note: Orectolobiformes and Squatinomorphs".

Teeth of "classic *Squatina*"-type morphology with long lateral wings devoid of lateral cusps are also represented in the Couches à Crassum, such as tooth Pl 12 C, D from Halanzy, assignable to *Squatina* according to Thies (1983: pl. 11 fig. 5-6) but rather identified as *Pseudorhina acanthoderma* (see Carvalho et al. 2008).

Remark - This taxon was not reported in the preliminary papers by Delsate *et al* 1989 nor Delsate & Lepage 1990.

Occurrence - Halanzy (Couches à Crassum); Kimmeridgian to Tithonian of Germany (Cappetta 2012).

Superorder Batomorphi Cappetta 1980
Order Rajiformes Berg, 1940
Family Toarcibatidae Greenfield, Delsate & Candoni, 2022

Remarks - The roots of these Toarcibatidae are at the holaulacorhize stage, i.e., between the two root lobes, the unique central foramen is in the centre of the labiolingual groove. The lobes are either separated in a V or in a line, depending on the mesio-distal extension of the teeth (see also Cappetta 2012: 397-400). In some specimens, the basilar groove tends to occlude and cover the median foramen.

The crown may be low with a low or strong crest and cuspidity. The uvula is always present but its origin and continuity from the lingual edge of the crown shows different generic patterns, with or without angulation, with or without horizontal rim or shoulder. The labial coronal apophysis may be strongly or weakly marked. Manzanares et al. (2018) studied the enameloid layer of Toarcibatidae and showed that it consists of a superficial single crystallite enameloid (SCE) with a parallel bundled enameloid (PBE) in all the taxa studied, but only in *Toarcibatis* and *Cristabatis* there exists a tangled bundled enameloid (TBE) underlying the latter, suggesting that the structural complexity and diversity of the Toarcibatidae are comparable to that recently described in others fossil batoids. The

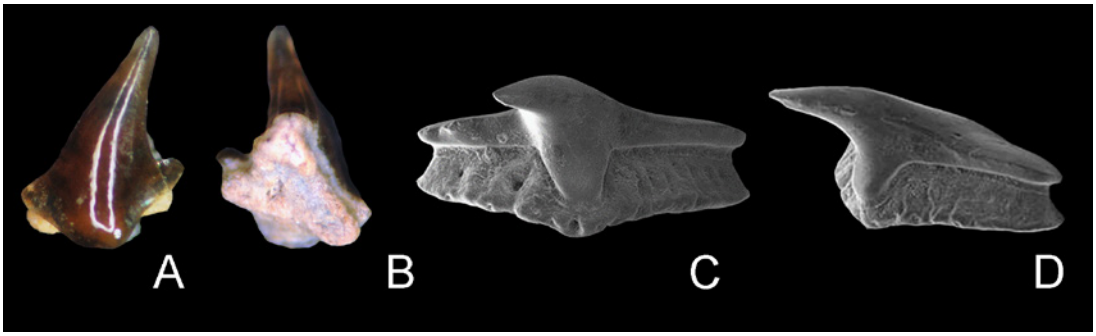


Plate 12: Genus *Pseudorhina*. A - TM586, *Pseudorhina alifera* (Münster 1842), A - labial view, B - lingual view; mesio-distal width: 1.2 mm; total height: 1.6 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). C, D - TM587, *Pseudorhina acanthoderma* (Fraas, 1854), C - lingual view, D - lingual oblique profile; mesio-distal width 1.7 mm; Halanzy, Couches à Crassum.

data of Manzanares et al. (2018) suggest a general trend towards simplification in batoid enameloid till the homogeneous single crystallite enameloid that is present in the majority of extant batoids, which contrasts with the increasing structural complexity seen in selachimorphs.

Here are some biostratigraphical data about the earliest Toarcibatidae:

- *Toarcibatis multicristata* Delsate & Candoni 2002: the Tenuicostatum Zone at Chassilé-la Vègre (Sarthe, F) yields the species *Toarcibatis multicristata* that persists near to *Toarcibatis brevicristata* in the Falcifer zone at Feuguerolles.
- *Toarcibatis brevicristata* Delsate & Candoni 2002: its stratum typicum is "Tc1b. Zone à Serpentinum, s.-Z. à Falciferum", and the locus typicus is Chaumitton (Sarthe, Normandy, France), in the upper part of the Sables et Calcaires de Saint-Rémy-du-Val described by Juignet *et al* 1984 : the lower part of this unit is composed of fine, clayey, micaceous sands, ochre to salmon in color, without fauna, attributed to the Tenuicostatum Zone; the upper part of the Calcaires de Saint-Rémy-du-Val is clayey and carbonaceous and contains the invertebrate fauna *Dactylioceras anguiformis*, *Dactylioceras* sp., *Harpoceras falciferum*, *Harpoceratoides* gr. *kisslingi*, *Nodocoeloceras crassoides*, *Orthildaites douvillei*, *Lobothyris* sp., *Zeilleria lycetti*, *Homoeorhynchia* aff. *cynocephala*, *Pholadomya* cf. *fidicula*, *Pholadomya* voltzi, *Pleuromya* sp., *Oxytoma* sp., *Pseudolimea duplicata*, *Camptonectes* sp., *Ctenostreon eleus*, signing the Serpentinus Zone. The washing and screening of this upper part (Serpentinus Zone) of the Calcaires de Saint-Rémy-du-Val yielded the Hybodontiform *Asteracanthus*, the Synechodontiform *Palidiplospinax* cf. *enniskilleni*, the Heterodontiform *Paracestracion* cf. *sarstedtensis*, Hemiscylliidae indet., and the Batomorph *Toarcibatis brevicristata* Delsate & Candoni 2001.

However, *T. brevicostata* persists near to *Cristabatis* cf. *crescentiformis* and *Toarcibatis* cf. *elongata* in the Bifrons Zone (at Feuguerolles), while these appear in Lorraine (B, L, F), from the top of the Bifrons Zone (Crassum layers) at Halanzy (B) and Zoufftgen (L), to the Thouarsense Zone (at Zoufftgen).

The two toarcibatid genera *Toarcibatis* and *Cristabatis* from Halanzy and Zoufftgen can be differentiated on profile views of the teeth.

Genus *Toarcibatis* Delsate & Candoni, 2001

Generic differential diagnosis - The lingual surface of the crown in profile is concave, and a well-marked glabellar rim surmounts the uvula.

Toarcibatis elongata Delsate & Candoni, 2001

Pl. 13 A-D

1989 *Protospinax* - Delsate et al.: pl. 1, fig. 2.

1990 Batomorphe - Delsate & Lepage: fig. 6.

2001 *Toarcibatis elongata* - Delsate & Candoni: p.135, fig.2.

2002 *Toarcibatis elongata* Delsate & Candoni: pl. I, fig. 5-8.

2012 *Toarcibatis elongata* - Cappetta 2012: p. 399, fig. 388.

Material - 18 teeth from Dudelange-Zoufftgen (including MnhnL TM235, TM589) and 80 teeth from Halanzy (including MnhnL TM588, TM590).

Occurrence - the level 6 (Variabilis Zone, Illustris and Variabilis subzones), 8 and 11 (Thouarsense zone, Thouarsense and Bingmanni subzones) of Dudelange-Zoufftgen (L); the Couches à Crassum of Belgian (Halanzy, Saint-Mard) and French (Mont-Saint-Martin, Longlaville) Lorraine; Bifrons to Thouarsense zones of Feuguerolles (Calvados, F).

Genus *Cristabatis* Delsate & Candoni, 2001

Generic differential diagnosis - The lingual surface of the crown is almost flat in profile and extends directly into the uvula, with a rim barely marked or absent.

Cristabatis crescentiformis Delsate & Candoni, 2001

Pl. 14 A-E

2001 *Cristabatis crescentiformis* - Delsate & Candoni: p. 135, fig. 2.

2002 *Cristabatis crescentiformis* - Delsate & Candoni: pl. I, figs 9-11.

2012 *Cristabatis crescentiformis* - Cappetta: p. 398, fig. 387.

Material - 2 teeth from Dudelange-Zoufftgen (including MnhnL TM591) and 20 teeth from Halanzy (including MnhnL TM592, TM593, TM594, TM595).

Occurrence - the level 11 (Thouarsense zone, Thouarsense and Bingmanni subzones) of Dudelange-Zoufftgen (L); the Couches à Crassum of Belgian (Halanzy, Saint-Mard) and French (Mont-Saint-Martin, Longlaville) Lorraine; the Bifrons to Thouarsense Zones of Feuguerolles (Calvados, F).

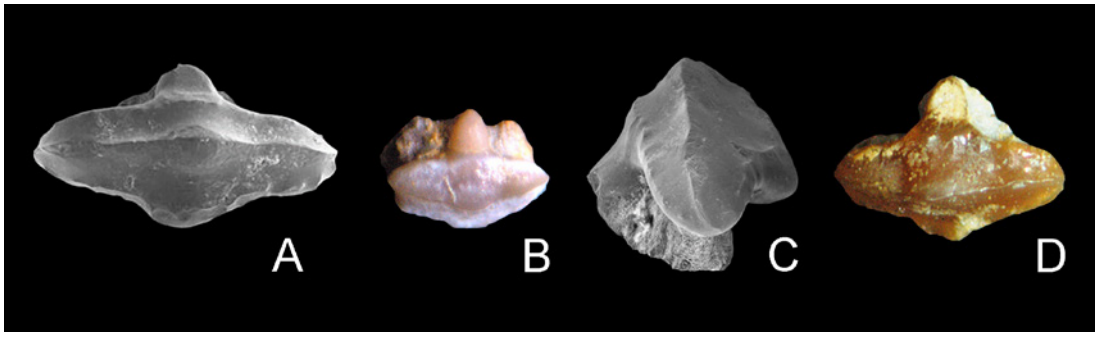


Plate 13: *Toarcibatis elongata* Delsate & Candoni 2001. **A** - TM588: apical view, mesio-distal width 1.6 mm; Halanzy, Couches à Crassum. **B** - TM589: apical view, mesio-distal width 0.8 mm; Dudelange-Zoufftgen, bed 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **C** - TM590, profile, mesio-distal width 0.85 mm; Halanzy, Couches à Crassum. **D** - TM235, apical view, mesio-distal width 1 mm; Dudelange-Zoufftgen, bed 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones).

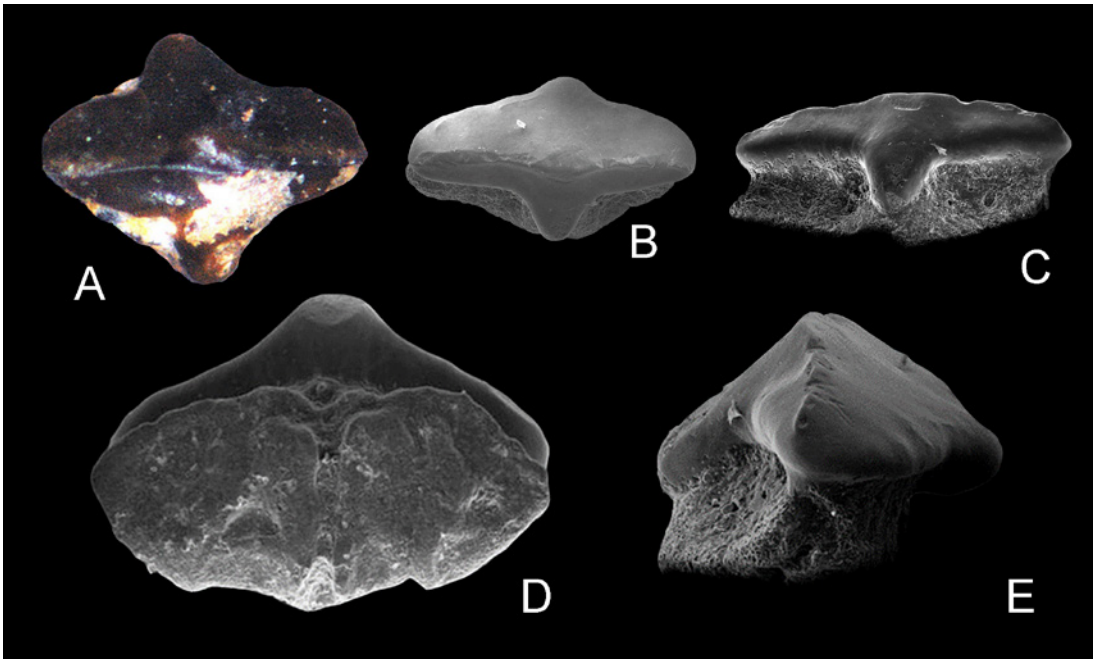


Plate 14: *Cristabatis crescentiformis* Delsate & Candoni 2001. **A** - TM591, apical view, mesio-distal width 1.0 mm; Dudelange-Zoufftgen, Level 11 (L2), (Thouarsense Zone, Thouarsense and Bingmanni subzones). **B** - TM592, apical view, mesio-distal width 1 mm; Halanzy, Couches à Crassum. **C** - TM593, lingual view, mesio-distal length 0.95 mm; Halanzy, Couches à Crassum. **D** - TM594, basal view, mesio-distal width 1.1 mm; Halanzy, Couches à Crassum. **E** - TM595, profile, labio-lingual length 0.7 mm; Halanzy, Couches à Crassum.

4 Discussion

The Toarcian fauna of southeast Belgium and Luxembourg perfectly illustrates the diversity increase of the Chondrichthyes towards the end of the Lower Jurassic. Following faunas consisting of Hybodontiformes, Synechodontiformes, Hexanchiformes and *Agaleus* Duffin & Ward, 1983, in the pre-Toarcian Jurassic, the Lower Toarcian, in the studied area represented by a condensation horizon between the top of the Tenuicostatum Zone and the base of the Serpentinum Zone, corresponding to the second step of the Toarcian oceanic anoxic event (T-OAE) (Thuy et al. 2025), saw the appearance of the Pseudonotidanidae *Welcommia terencei* Delsate & Godefroit, 1995 (see Klug & Kriwet 2010) alongside *Hybodus hauffianus* Fraas, 1895, *Palidiplospinax* cf. *occultidens* Duffin & Ward, 1993, and *Palidiplospinax* cf. *enniskilleni* Duffin & Ward, 1993. The following Serpentinum and Bifrons zones, witnessing phases of hypoxic to anoxic bottom-water conditions in the study region, yielded only *Hybodus hauffianus* and rare Synechodontiformes, contrasting with abundant and diverse Actinopterygians especially in the Exaratum subzone, corresponding to the 3rd and 4th steps of the T-OAE (Thuy et al. 2025).

At the boundary between the Bifrons and Variabilis zones, the condensation horizon called 'Couches à Crassum' in the study area has yielded a highly diverse fauna of Neoselachii ('Lorraine-type' shark and ray fauna) with *Protospinax*, the Heterodontiform *Paracestracion*, the Squatiniform *Pseudorhina*, the already highly diverse group of Orectolobiformes with *Palaeobrachaelurus alisonae*, *P. aperizostus*, *P. vanessae* nov. sp., *Annea maubeugei*, *Ornatoscyllium* cf. *pattersoni*, *Eoscyllium (Heterodontus) duffini*, *Thiesoscyllium underwoodi* nov. gen. nov. sp., the Galeomorphi indet. *Jurobatos cappettai*, as well as abundant and already diversified batomorphs Toarcibatidae. The latter association is already present in the Serpentinum Zone at Feuguerolles (Normandy) and anticipated by an upper Pliensbachian (Spinatum Zone) Batomorphii (*Antiquaobatis grimmenensis*) from Grimmen in north-eastern Germany (Stumpf & Kriwet 2019).

An assemblage very similar to those recorded from the 'Couches à Crassum' is here presented from the Crassum Schichten (levels 4, top of Bifrons Zone, & 5, base of Variabilis Zone) to the slightly younger Thouarsense zone of Dudelange-Zoufftgen (L) in more oxygenated sediments than in other parts of the study area.

The upper Toarcian (Aalensis Zone, Mactra Subzone) of Dudelange-Ginzebierg (L) (Delsate 2003) yielded *Asteracanthus* sp., (Delsate 2003: Pl. 1 Fig. 1-3: sensu Agassiz 1837 – see Kriwet et al. 1997: p. 8-10, Fig. 5a), *Lissodus guenneguesi* Delsate, 2003 Pl. 2 Figs. 3-10, Toarcibatidae *Doliobatis weisi* Delsate & Candoni, 2002, Orectolobiformes among which *Palaeobrachaelurus vanessae* nov. sp., and the galeomorph cf. Orectolobiformes *Microtoxodus* Delsate, 2003, and *Folipistrix* Kriwet, 2003, that has not been identified in earlier deposits in Lorraine.

Thus, most of the extant groups of elasmobranchs were established by the Toarcian, with two particularly diverse groups, the Toarcibatidae rays (anticipated by a form from the Pliensbachian, see Stumpf & Kriwet 2019) and the Orectolobiformes.

Biostratigraphical and geographical faunal comparisons (see Delsate & Weis 2010) with Alsace, Nivernais, Calvados-Normandy, Deux-Sèvres, and Hungary allow the following conclusions (Fig. 1; Tables 1 and 2):

- Most of the 'Lorraine-type' shark and ray fauna occurring at the top of the Bifrons Zone (in Lorraine and Alsace, in shallow epicontinental marginal/littoral settings (Delsate & Weis 2010: p. 49)) was already present and co-occurring with abundant *Sphenodus* in the Serpentinum Zone of Normandy in well-oxygenated shallow epicontinental settings (unpublished data collected in collaboration with Laurent Candoni and Marc Chesnier). Variations in seawater temperature, especially the large-scale warming events in the basal Toarcian and in the middle of the Bifrons zone (Dera et al. 2009) may also have contributed to these faunal changes. The fauna is also already partially present in the Serpentinum Zone in open marine deep-water settings of the Gerecse mountains in Hungary (work in progress with Istvan Zentai and Attila Fitos) together with abundant *Sphenodus* and the Pseudonotidanidae *Welcommia terencei*.

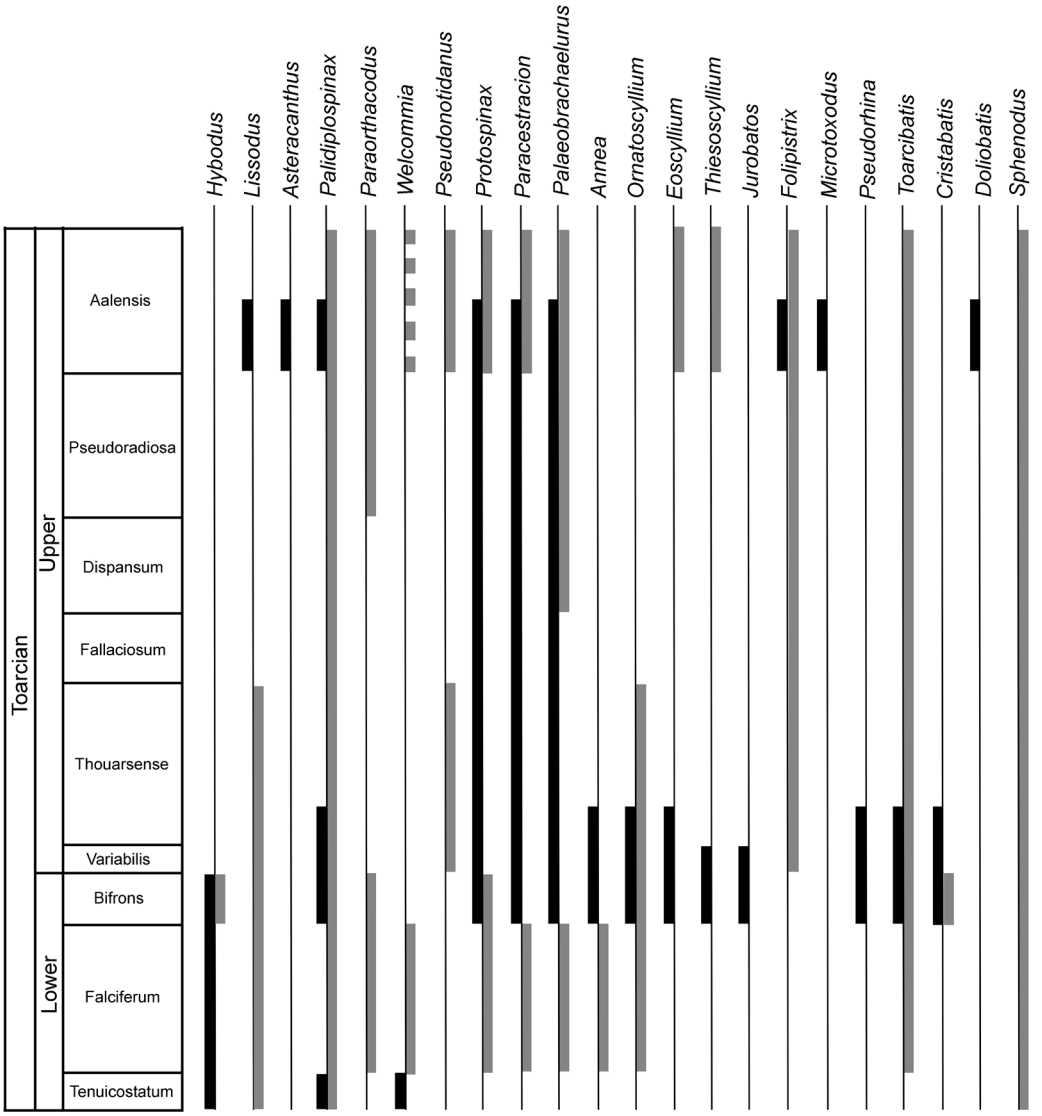


Fig. 1: Stratigraphic range chart of the chondrichthyan genera included in tables 1 and 2, with occurrences in Lorraine localities (Ottemt, B, the Bascharage-Sanem-Zolver-Belvaux area, L, Halanzy, B, Dudelange-Zoufftgen, L and Ginzebierg, L) in black and occurrences in Calvados (Feuguerolles, F) and Deux-Sèvres (Nanteuil, F) in grey.

- In the Bascharage section (Thuy et al. 2025), the base of the Serpentinum Zone coincides with the 2nd step of the negative carbon isotope excursion of the Toarcian oceanic anoxic event (T-OAE). If the strong diversity of the Actinopterygians (Delsate 1999) in the Exaratum Subzone may be linked to the first sea water temperature increase corresponding to the T-OAE, the high diversification of Neoselachians in Lorraine does not follow immediately the T-OAE but rather the second temperature rise, at the end of the Bifrons Zone.
- The 'Lorraine-type' shark and ray fauna of the upper Bifrons Zone persists into and further evolves in the upper Toarcian of Dudelange-Zoufftgen (L) as well as in the upper Toarcian

Table 1: Distribution of the Chondrichthyan taxa in the Lorraine localities: Ottemt (B), the Bascharage-Sanem-Zolver-Belvaux area (L), Halanzy (B), Dudelange-Zoufftgen (L) and Ginzebierg (L).

	OTTEMT (B)	**BASCHARAGE, SANEM, ZOLVER, BELVAUX (L)**	**HALANZY, SAINT-MARD (B)**	**ZOUFFTGEN (L)**		**GINZEBIERG (L)**
				Levels 4-7	**Levels 8-12**	
	Tenuicostatum	**Falcifer – Bifrons**	**Couches à Crassum: Top Bifrons – Base Variabilis**	**Crassum Schichten: Bifrons-Variabilis-Illustris**	**Thouarsense-Bingmanni**	**Aalensis**
Hybodus hauffianus	x	x				
Hybodus sp.	x					
Hybodontidae indet.			x	x	x	
Lissodus guenneguesi						x
Asteracanthus sp.						x
Welcommia terencei	x					
Palidiplospinax enniskilleni	x		x	x	x	
Palidiplospinax occultidens	x					
Synechodontiforms indet.		x				x
Protospinax cf. *magnus*			x	x	x	
Protospinax sp.						x
Paracestracion sarstedtensis			x	x	x	
Paracestracion sp.						x
Palaeobrachaelurus cf. *aperizostus*			x	x	x	
Palaeobrachaelurus sp.						x
Palaeobrachaelurus alisonae			x	x	x	
Palaeobrachaelurus cf. *alisonae*			x			
Palaeobrachaelurus vanessae			x	x	x	x
Annea maubeugei			x		x	
Ornatoscyllium pattersoni			x		x	
Eoscyllium duffini			x	x	x	
Thiesoscyllium underwoodi			x			
Jurobatos cappettai			x	x		
Microtoxodus & *Folipistrix*						x
Pseudorhina acanthoderma			x			
Pseudorhina alifera					x	
Toarcibatis elongata			x	x	x	
Cristabatis crescentiformis			x	x	x	
Doliobatis weisi						x

Table 2: Occurrences of the "Lorraine-type" shark fauna in Feuguerolles (Calvados) and Nanteuil (Deux Sèvres).

	Feuguerolles								Nanteuil
	T1abc Tenui-costatum	**T2-T7-T8/1 Serpentinum**	**T8/2-T8/5 Bifrons**	**T9-T10 Variabilis**	**T11-T12 Thouarense**	**T12 Dispansum**	**T13 Pseudo-radiosa**	**T14 Aalensis**	**Aalensis**
Hybodus sp.			x						
Lissodus sp.	x	x	x		x				
Palidiplospinax	x	x	x	x	x	x	x	x	x
Pseudonotidanus cf. *semirugosus*				x	x				x
Welcommia terencei		x							x ?
Sphenodus sp.	x	x		x	x	x	x	x	
Paraorthacodus		x	x				x		x
Protospinax		x	x						x
Paracestracion sp.		x							x
Ornatoscyllium		x	x	x	x				
Annea sp.		x							
Palaeobrachaelurus sp.		x				x		x	
Palaeobrachaelurus alisonae									x
Eoscyllium duffini					x			x	x
Thiesoscyllium underwoodi									x
Folipistrix sp.				x	x	x	x	x	x
Toarcibatis alticarinata			x			x			x
Toarcibatis brevicristata		x	x						
Toarcibatis multicristata		x							
Toarcibatis elongata			x	x					
Cristabatis sp.			x						

and Aalenian of Nanteuil (Deux Sèvres, western France) together with abundant Pseudonotidanidae (*Pseudonotidanus* sp.) and *Sphenodus* (collaboration with Michel Cougnon, André Lacroix and Jérôme Caillet).

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Marshall C. R. 1987. - Lungfish: phylogeny and parsimony, in Bernis W. E., Burggren W. W. & Kemp N. E. (eds), The Biology and Evolution of Lungfishes, Journal of Morphology 1: 151-152.

Röckel D., Korn W. & Kohn A. J. 1995. - Manual of the Living Conidae. Volume 1: Indo-Pacific Region. Christa Hemmen, Wiesbaden, 517 p.

Schwaner T. D. 1985. - Population structure of black tiger snakes, *Notechis ater niger*, on off-shore islands of South Australia: 35-46, in Grigg G., Shine R. & Ehmann H. (eds), Biology of Australasian Frogs and Reptiles. Surrey Beatty and Sons, Sydney.

Gerecke R., Stoch F., Meisch C. & Schrankel I. 2005. - Die Fauna der Quellen und des hyporheischen Interstitials in Luxemburg unter besonderer Berücksichtigung der Milben (Acari), Muschelkrebse (Ostracoda) und Ruderfusskrebse (Copepoda). Ferrantia 41, Musée national d'histoire naturelle, Luxembourg, 140 p.

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