

Morphological variations and geographic distribution of the rare Middle Jurassic ammonite *Oecoptychius refractus*

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The rare Middle Jurassic ammonite *Oecoptychius refractus* is revisited based on material collected in southern Poland (Ogrodzieniec quarry) and France (St.-Laon near Loudun, western France). Based on available data and an evaluation of the literature, *O. refractus* ranges from the middle Callovian *Kosmoceras jason* Zone to the upper Callovian *Quenstedtoceras lamberti* Zone. Additionally, two specimens from Kachchh (western India) were re-evaluated and are now assigned to the lower part of the upper Callovian *Peltoceras athleta* Zone, similar to specimens from southern Germany. In the present study, *O. refractus* displays large morphological variation in the shape of the body-chamber, with a gradation from V- to U-shape. Additionally, the smaller upper Callovian specimens from Poland are morphologically closer to the lectotype (more evolute and compressed) and form a separate grouping as compared to the much larger middle Callovian specimens from France. Based on available data, the authors tentatively propose *Phlycticeras polygonium* var. *waageni* [M] as the dimorphic partner of *O. refractus* [m]; both dimorphs have similar morphology (ribbing pattern and striations), suture line and co-occur from middle to upper Callovian. *Oecoptychius refractus* maintains its morphological variability throughout the middle and upper Callovian, before its final disappearance in the *Q. lamberti* Zone. *Oecoptychius refractus* is better documented from western Tethyan localities (Poland, Germany and France) as compared to those from the eastern Tethys (Madagascar and India). Recurrent sea level rises in the Middle Jurassic might be one of the plausible factors for its extensive palaeobiogeographic range.

Key words: Ammonoidea, *Oecoptychius*, morphological variation, Callovian, Jurassic, Tethys, Poland.

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Introduction

The species of the Middle Jurassic ammonite genus *Oecoptychius* Neumayr, 1878, are quite rare forms spanning from the upper Bajocian *Garantiana garantiana* Zone up to the basal part of the upper Callovian *Peltoceras athleta* Zone (Schweigert and Dietze 1998; Schweigert et al. 2003). However, their occurrences in the *P. athleta* Zone are excessively rare with only two records from the basal part of the *P. athleta* Zone; one from Sengenthal in the eastern Franconian Alb, southern Germany (Callomon et al. 1987: pl. 3: 7) and the other one from Kachchh, western India

(Spath 1928: 278, pl. 81: 5). To date there are no published records younger than the upper Callovian *Hecticoceras trezeense* Subzone in the basal part of the *P. athleta* Zone (Schweigert and Dietze 1998).

Here we document the first *Oecoptychius refractus* (Reinecke, 1818) from southern Poland found in a condensed bed (upper Callovian–lower Oxfordian) of the Ogrodzieniec quarry (Fig. 1A–D) (see also Jain et al. 2022a, b). The paper also re-describes the morphology of *O. refractus* in detail and the morphological variation noted within this species based on specimens from the condensed bed of the Ogrodzieniec quarry and from the middle Callovian *Kos-*

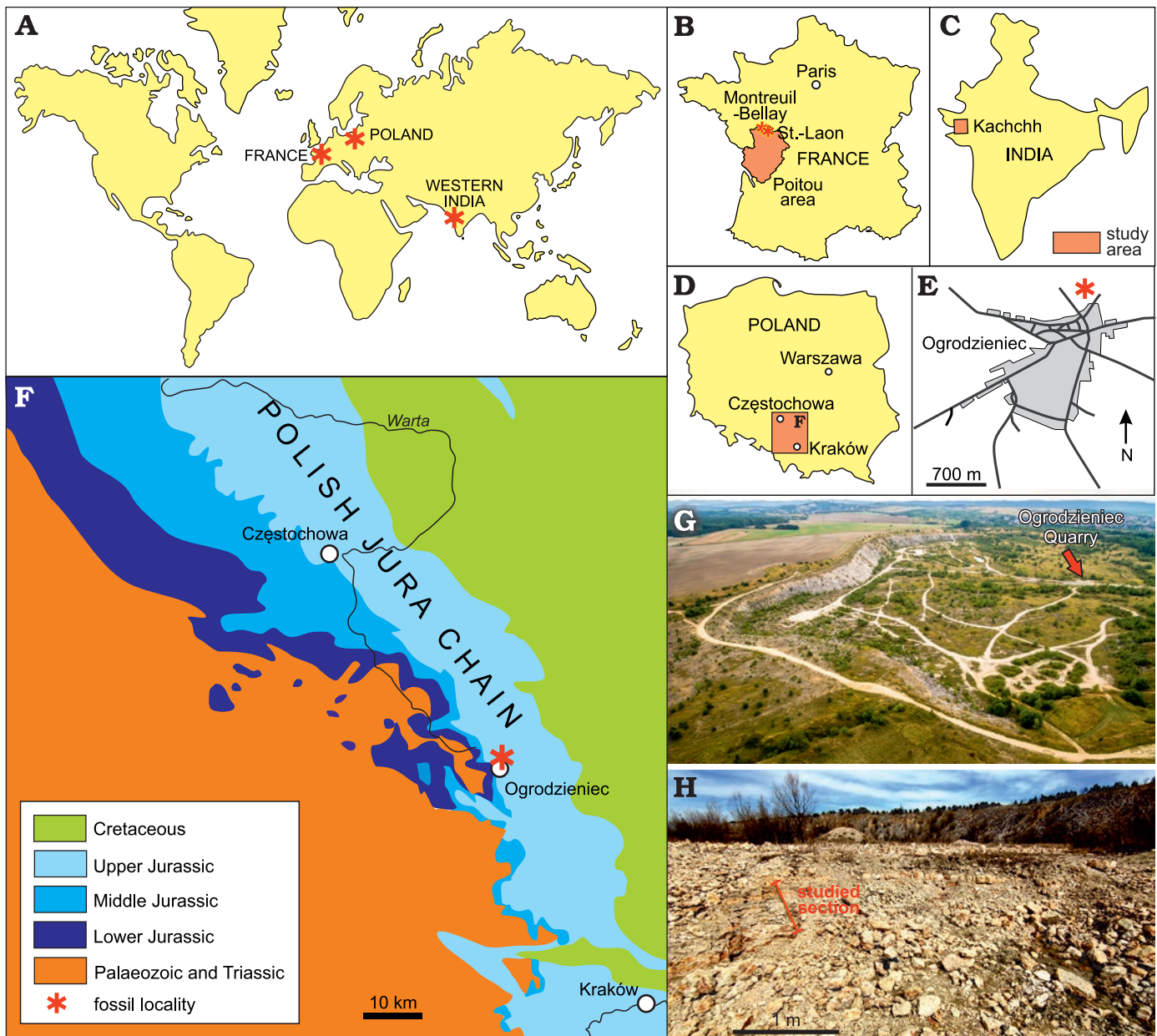


Fig. 1. Geological map and the abandoned Ogródzieniec quarry. **A.** Map showing the studied localities in Poland, western France, and Kachchh (western India). **B.** Map of France showing the position of St-Laon and Montreuil-Bellay. **C.** Map of India showing the position of Kachchh. **D.** Map of Poland showing the the position of Ogródzieniec. **E.** Detailed location of Ogródzieniec quarry (modified after Jain and Mazur 2021). **F.** Geological map of the Polish Jura Chain showing the location of the studied Ogródzieniec quarry. **G.** Aerial view of the Ogródzieniec quarry; arrow marks the location of the studied section. **H.** Exposure of the studied section.

moceras jason Zone of western France. Other occurrences from southern Germany as well as from Madagascar and western India are also taken into account. The present paper also re-evaluates the age of its occurrence in Kachchh (western India).

Oecoptychius refractus is the only species of *Oecoptychius* recorded from the upper Callovian above which the genus disappears from the fossil record (Schweigert and Dietze 1998). Thus, understanding the morphological changes of *O. refractus* from the middle to upper Callovian is of interest as it may provide some better understanding

of the morphological changes within the genus during its demise.

Institutional abbreviations.—BSPM, Bayerische Staatssammlung für Paläontologie, München, Germany; GIUS, Institute of Earth Sciences of the University of Silesia in Katowice, Poland; NMC, Naturkundemuseum Coburg, Germany; SMNS, Staatliches Museum für Naturkunde Stuttgart, Germany.

Other abbreviations.—D, diameter of the shell; H, height of the whorl; [m], microconch; [M], macroconch; T, thickness of the whorl; U, umbilicus.



Fig. 2. Lithostratigraphy and biostratigraphy at the Ogradzieniec quarry (modified after Dembicz et al. 2006). Arrow shows the occurrence of *Oecoptychius refractus* (Reinecke, 1818) within the general stratigraphy of the Ogradzieniec quarry. Bed numbers (1, 1a, 2, 3, 18, and 37) after Dembicz et al. (2006).

Geological setting

Ogradzieniec quarry, Poland.—The Ogradzieniec quarry displays a section with a stratigraphic condensation in glauconitic marl and glauconitic limestone beds ranging the upper Callovian to lower Oxfordian (see also Barski et al. 2004; Dembicz et al. 2006; see Fig. 2).

The present study is based on new collections from this locality, from the condensed glauconitic nodular oolitic limestone bed β of Główniak (2012) (Fig. 1). Associated ammonites indicate *Quenstedtoceras lamberti* Subzone (*Q. lamberti*

Zone; upper Callovian) to *Cardioceras bukowskii* Subzone (*Cardioceras cordatum* Zone; lower Oxfordian), and include *Peltoceras schroederi*, *Hibolithes hastatus* (a large specimen attached to *P. schroederi*), *Quenstedtoceras lamberti*, *Kosmoceras duncani*, *Peltoceratoides (Peltoceratoides) williamsoni*, *Peltoceratoides (Parawedekindia) arduennensis*, *Euaspidoceras babeanum*, *Bukowskites minax*, *Hecticoceras (Putealicerias) punctatum*, and *Euaspidoceras subbabeanum* sensu Jeannet (1951) and several fragmentary specimens of *Cardioceras* sp. (Fig. 3) (see also Jain et al. 2022a, b).

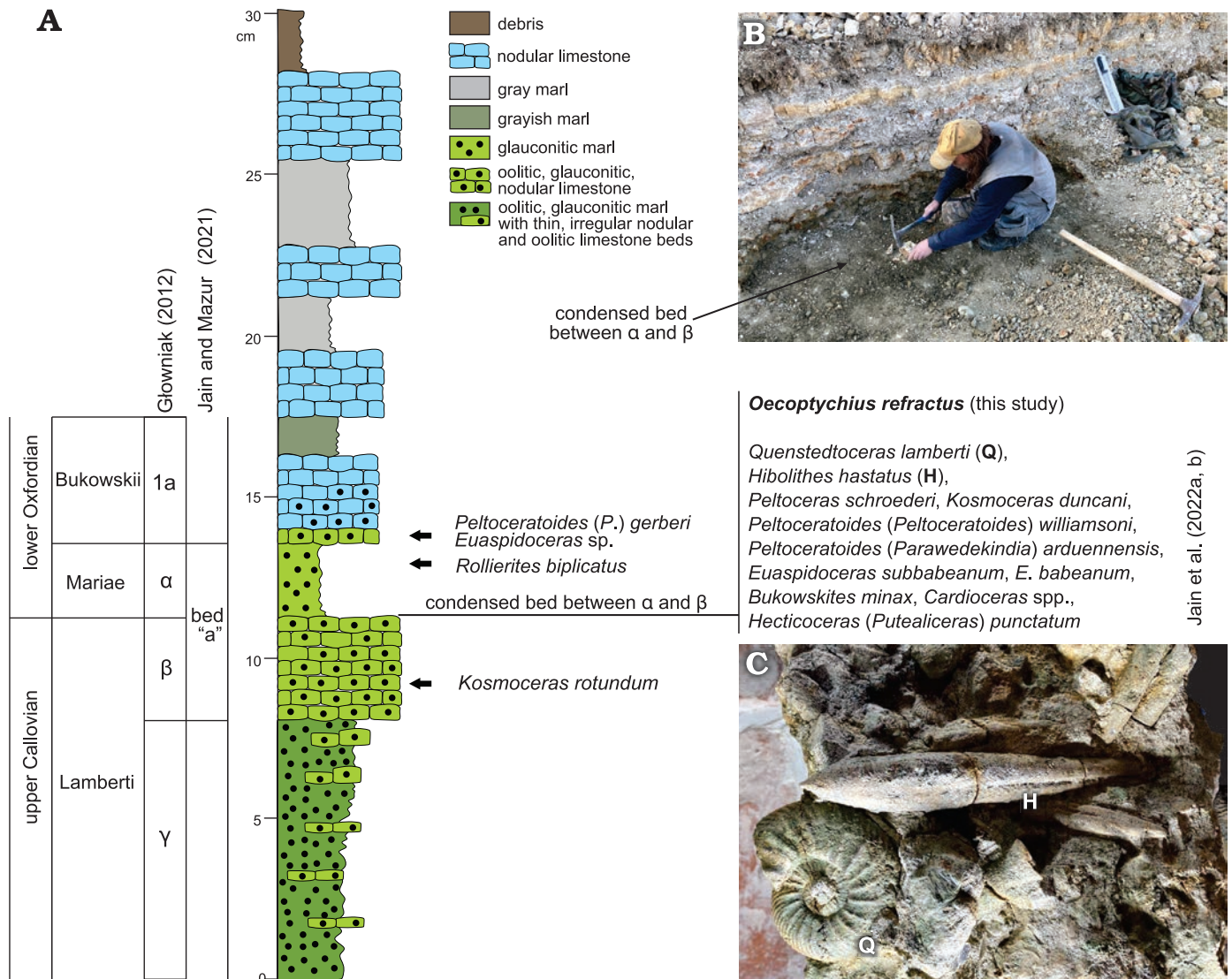


Fig. 3. Biostratigraphy of the studied section. **A**. Geological column, correlation of studied beds with these of Główniak (2012) and the occurrence of specimens noted in the present study (modified after Jain and Salamon 2023). **B**. Field photo of the condensed bed where the studied specimens of *Oecoptychius refractus* (Reinecke, 1818) [m] were recorded. **C**. Close-up of the block with *Quenstedtoceras lamberti* (Q) and *Hibolithes hastatus* (H).

Jain and Mazur (2021), recorded the dimorphic pairs of *Rollierites biplicatum* from the upper part of bed "a" and *Kosmoceras rotundum* in its lower part (bed β of Główniak 2012). They assigned their bed "a" to the *Quenstedtoceras lamberti* Zone (upper Callovian; Fig. 3A).

Later, Jain et al. (2022a, b) recorded the presence of *Peltoceras schroederi* with *Kosmoceras rotundum* and *K. duncani* from the condensed bed between bed α and β within bed "a" of Główniak (2012). This condensed bed also yielded lower Oxfordian *C. bukowskii* Subzone, *C. cordatum* Zone (lower Oxfordian) forms such as *Euaspidoceras babeianum*, *Bukowskites minax*, *Peltoceratoides (Peltoceratoides) arduennensis*, *P. (P.) williamsoni*, and *Cardioceras* sp. Based on the strength of *P. schroederi* with *Kosmoceras rotundum* and *K. duncani* from the lower part of bed "a", Jain et al. (2022a, b) assigned bed "a" to the *Peltoceras athleta* Subzone (*Peltoceras athleta* Zone, upper Callovian). However, both *P. schroederi* and *K. duncani* have been documented to

occur within the above *Quenstedtoceras lamberti* Zone of the upper Callovian as well (Bonnot 1995; Courville and Bonnot 1998; Bonnot and Cariou 1999; Fortwengler et al. 1997; Lebrun and Courville 2013; Pellenard et al. 2014).

Hence, based on new field data and published ammonite records, we concur with Jain and Mazur (2021) in the assignment of the lower part of bed "a" exposed in the Ogródzieniec quarry (i.e., bed β of Główniak 2012) to the *Quenstedtoceras lamberti* Subzone, *Q. lamberti* Zone of the upper Callovian (Fig. 3).

Główniak (2012) noted that in the Ogródzieniec section, the contact between the upper Callovian and the lower Oxfordian runs within bed α (see Figs. 1, 3). Bed α is equivalent to bed 16 of Dembicz et al. (2006) which yielded reworked ammonites of both the upper Callovian *Quenstedtoceras lamberti* Zone and the lower Oxfordian *Quenstedtoceras mariae* Zone, i.e., *Quenstedtoceras lamberti* and *Quenstedtoceras mariae*, respectively. Główniak (2012) assigned the basal

sediments (bed γ) exposed in the Ogródzieniec quarry to the *Peltoceras athleta* Zone but provided no information about the faunal content (Fig. 3). In this regard, current study could assume that the occurrence of *Oecoptychius refractus* in the Ogródzieniec quarry (Fig. 3) could be the highest occurrence of *Oecoptychius* as this genus does not range above the *Hecticoceras trezeense* Subzone, *Peltoceras athleta* Zone, upper Callovian (see Schweigert and Dietze 1998). However, the ammonite assemblage occurring with *O. refractus* within the bed “a” in Ogródzieniec quarry is overwhelmingly in favour of the *Q. lamberti* Subzone, *Q. lamberti* Zone, upper Callovian (Fig. 3). This could mean that *O. refractus* occurrence in the Ogródzieniec quarry is stratigraphically the highest worldwide. Alternatively, it could mean faunal elements within condensed horizon between beds β and α indicate also *Peltoceras athleta* Zone, upper Callovian as well. More sampling across the Ogródzieniec quarry is required to answer this question. For now, the range of *O. refractus* is extended well into the *Q. lamberti* Zone of the upper Callovian.

Poitou area, western France.—The Callovian succession Poitou area consists of a thin ferruginous oolite beds which are very rich in ammonites and other invertebrates. At St.-Laon near Loudun (see Fig. 1B), oolitic limestone beds of the middle Callovian *Kosmoceras jason* and *Erymnoceras coronatum* zones have been especially well sampled. Specimens of *O. refractus*, as well as their dimorphic coun-

terpart *Phlycticeras* spp. are rather common there and often preserved as inner moulds, sometimes even with impression of the lapped aperture (Schweigert and Dietze 1998). The sample of *O. refractus* studied herein originates from the *Kosmoceras jason* Zone from St.-Laon near Loudun (see Fig. 1B). *Oecoptychius refractus* is present in the basal horizon of the *Peltoceras athleta* Zone, upper Callovian, which is best developed in the vicinity of Montreuil-Bellay (see Fig. 1B), but has become excessively rare (Schweigert et al. 2003; Bonnot et al. 2005). In higher levels of the *P. athleta* Zone, upper Callovian, *Oecoptychius* and *Phlycticeras* apparently disappear.

Kachchh, western India.—Spath (1928: 278, pl. 81: 5a–c) recorded two specimens of *Oecoptychius refractus* [m] (V-shaped body-chamber) with *Phlycticeras waageni* [M] (*Phlycticeras polygonium* var. *waageni* of Jain 2017: fig. 13f–n) (see also Waagen 1875: 40, pl. 9: 2a–c; Spath 1928: 91). The specimens were collected from the bed no. 2 of Raj Nath (1942), a characteristic marker bed within the Kachchh Basin that has also yielded *Peltoceras athleta* (see also Jain and Pandey 2000; Fürsich et al. 2001; Jain 1997, 2017). Beds just above this bed no. 2 have yielded the characteristic form of *Collotia fraasi* of the *Collotia collotiformis* Zone (see also Jain and Pandey 2000; Jain 2017), thus, limiting the stratigraphic occurrences of *Phlycticeras polygonium* var. *waageni* [M]–*Oecoptychius refractus* [m] to the *Hecticoceras*

Table 1. Dimensions of *Oecoptychius refractus* (Reinecke, 1818), specimens considered in the present study. Abbreviations: D, diameter of the shell; H, height of the whorl; T, thickness of the whorl; U, umbilicus; U/D, coiling ratio (umbilicus/diameter); T/H, relative whorl thickness (thickness of whorl/height of whorl).

Specimen no.	D	H	T	U	U/D	T/H	Illustration (if any)
Poland (upper Callovian)							
GIUS 8-3657/1	20.6	6.9	9.8	0.60	0.03	1.42	Fig. 4A ₁ –A ₄
GIUS 8-3657/6	11.3	5.6	7.2	0.90	0.08	1.27	Fig. 4B ₁ –B ₃
GIUS 8-3657/7	18.7	6.2	8.7	0.94	0.05	1.42	Fig. 4C ₁ –C ₄
GIUS 8-3657/8	14.1	4.9	7.1	0.60	0.04	1.46	Fig. 4D ₁ –D ₄
GIUS 8-3657/9	12.7	5.0	7.8	0.50	0.04	1.55	Fig. 5A ₁ –A ₄
GIUS 8-3657/10	15.7	–	–	–	–	–	Fig. 5B ₁ , B ₂
GIUS 8-3657/11	15.9	5.6	8.6	–	–	1.54	Fig. 5C ₁ –C ₄
GIUS 8-3657/2	15.5	6.8	9.3	0.80	0.05	1.38	Fig. 5D ₁ –D ₄
GIUS 8-3657/12	12.5	6.5	8.0	–	–	1.23	Fig. 6A ₁ –A ₃
GIUS 8-3657/5	11.5	5.5	7.2	0.60	0.05	1.31	Fig. 6B ₁ –B ₃
GIUS 8-3657/3	13.0	5.1	9.8	0.40	0.03	1.93	Fig. 6C ₁ –C ₃
GIUS 8-3657/4	15.1	5.6	8.1	0.70	0.05	1.44	Fig. 6D ₁ –D ₃
France (middle Callovian) (after Schweigert and Dietze 1998)							
Lectotype, NMC 52/1	12.1	6.8	8.8	0.50	0.04	1.29	Schweigert and Dietze 1998: pl. 9: 10
SMNS 63459/1	22.5	7.0	9.0	0.50	0.02	1.29	Schweigert and Dietze 1998: pl. 9: 4
SMNS 63458/1	21.2	6.0	9.0	–	–	1.50	Schweigert and Dietze 1998: pl. 9: 6
SMNS 63460/1	20.5	5.7	8.5	–	–	1.49	Schweigert and Dietze 1998: pl. 9: 7
SMNS 63457/1	16.8	6.2	8.0	0.30	0.02	1.29	Schweigert and Dietze 1998: pl. 9: 8
BSPM 1989 J 37	23.0	6.0	9.3	0.20	0.01	1.55	Schweigert and Dietze 1998: pl. 9: 11
SMNS 63458/2	21.0	7.3	11.0	0.50	0.02	1.51	–
SMNS 63460/2	20.3	6.3	8.5	0.50	0.02	1.35	–
SMNS 63460/3	17.5	6.3	8.2	0.50	0.03	1.30	–
SMNS 63460/4	17.0	6.7	9.8	–	–	1.46	–
SMNS 63457/2	16.0	7.0	8.3	–	–	1.19	–

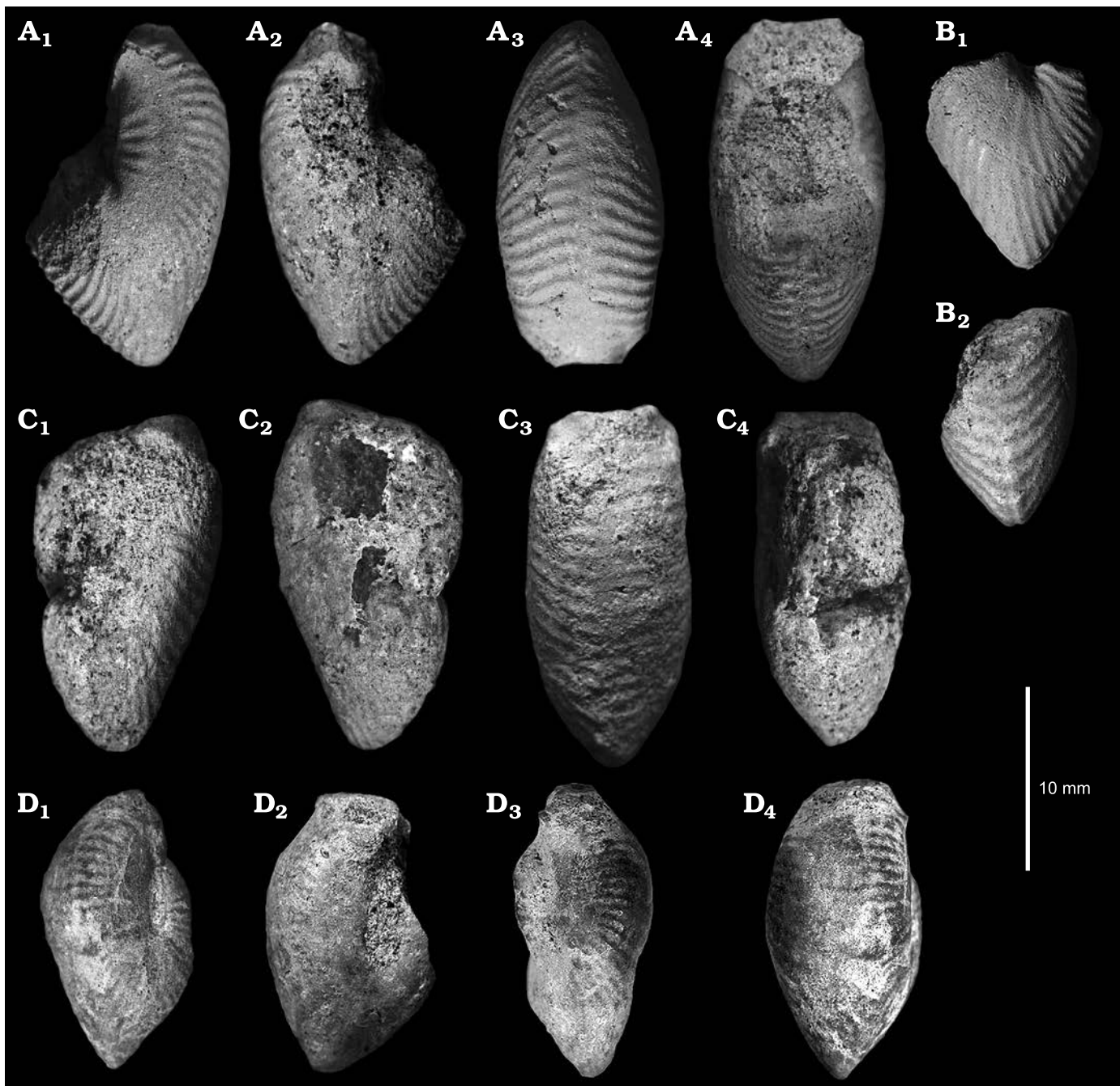


Fig. 4. Strigoceratid ammonoid *Oecoptychius refractus* (Reinecke, 1818) [m] from Ogrodzieniec quarry, *Quenstedtoceras lamberti* Zone, upper Callovian. A. GIUS 8-3657/1 in lateral (A₁), opposite lateral (A₂), ventral (A₃), and dorsal (A₄) views. B. GIUS 8-3657/6 in lateral (B₁) and ventral (B₂) views. C. GIUS 8-3657/7 in lateral view (C₁), detail showing the smooth umbilical region (C₂), opposite lateral (C₃) and dorsal (C₄) views. D. GIUS 8-3657/8 in lateral (D₁), opposite lateral (D₂), ventral (D₃), and dorsal (D₄) views.

trezeense Subzone, lowermost *Peltoceras athleta* Zone, upper Callovian, in Kachchh, as also suggested by Schweigert and Dietze (1998) from Europe.

Material and methods

A total of 29 specimens of *Oecoptychius refractus* were studied (Figs. 4–10; see Table 1); 12 specimens from the Ogrodzieniec quarry (MAS collection, GIUS 8-3657/1–12;

Figs. 4–6) housed at the University of Silesia in Katowice, Faculty of Natural Sciences, Institute of Earth Sciences, Sosnowiec, Poland, and 17 specimens from St.-Laon near Loudun, Poitou area, France (Rolf Mitschelen collection, SMNS 70655/1–17; Fig. 7B) housed at the State Museum of Natural History, Stuttgart, Germany.

The Kachchh (western India) specimens of *Phlycticeras polygonium* var. *waageni* [M] (see Jain 2017: fig. 131–n, f–h; refigured here as Fig. 11B₁–B₄, G, H, respectively) are

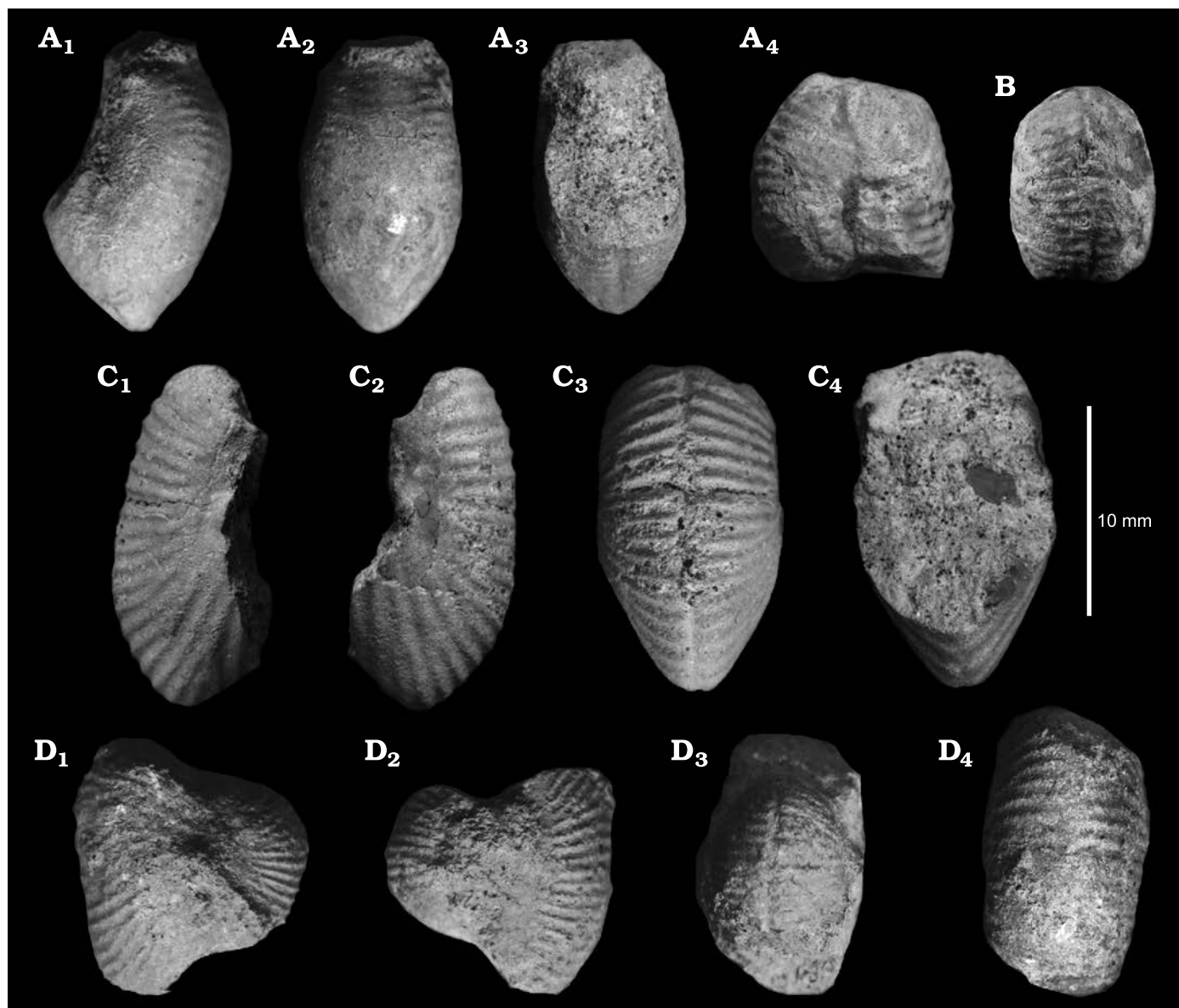


Fig. 5. Strigoceratid ammonoid *Oecoptychius refractus* (Reinecke, 1818) [m] from Ogrodzieniec quarry, *Quenstedtoceras lamberti* Zone, upper Callovian. A. GIUS 8-3657/9 in lateral (A₁), dorsal (A₂), ventral (A₃), and dorsal (A₄, note the ribbing pattern) views. B. GIUS 8-3657/10 in ventral view. C. GIUS 8-3657/11 in lateral (C₁), opposite lateral (C₂), ventral (C₃), and dorsal (C₄) views. D. GIUS 8-3657/2 in lateral (D₁), opposite lateral (D₂), ventral (D₃), and dorsal (D₄) views.

cataloged as SJ/JA/99-00/23 and Ju/B44/1, respectively, and kept at the Department of Geology, Rajasthan University (Rajasthan, India).

All measurements (Table 1) were taken using a caliper from the specimens and photographed using Canon D530 camera. Images were prepared using Adobe Photoshop CS6 and CorelDRAW version 21.

Systematic palaeontology

Family Strigoceratidae Buckman, 1924

Subfamily Phlycticeratinae Spath, 1925

Genus *Oecoptychius* Neumayr, 1878

Type species: Nautilus refractus Reinecke, 1818, middle Callovian, *Erymnoceras coronatum* Zone, eastern Franconian Alb (Trockau, Germany).

Oecoptychius refractus (Reinecke, 1818)

Figs. 4–10.

1818 *Nautilus refractus*; Reinecke 1818: fig. 27–30.

1830 *Ammonites refractus* Reinecke; Zieten 1830: 14, pl. 10: 9.

1846 *Ammonites refractus* Reinecke; Quenstedt 1846: 150, pl. 11: 12.

1857 *Ammonites refractus*; Quenstedt 1857: 524, pl. 69: 25, 26, 28–30.

1878 *Oecoptychius refractus*; Neumayr 1878: 73.

1887 *Ammonites refractus*; Quenstedt 1887: 762f, pl. 86: 37–50.

1887 *Oecoptychius refractus* Quenstedt; Zakrzewski 1887: 122, pl. 1: 3.

1897 *Oecoptychius refractus* Haan; Glangeaud 1897: 104, pl. 3: 7–10.

1908 *Ammonites (Oecoptychius) refractus* Reinecke sp.; Engel 1908: pl. 4: 6.

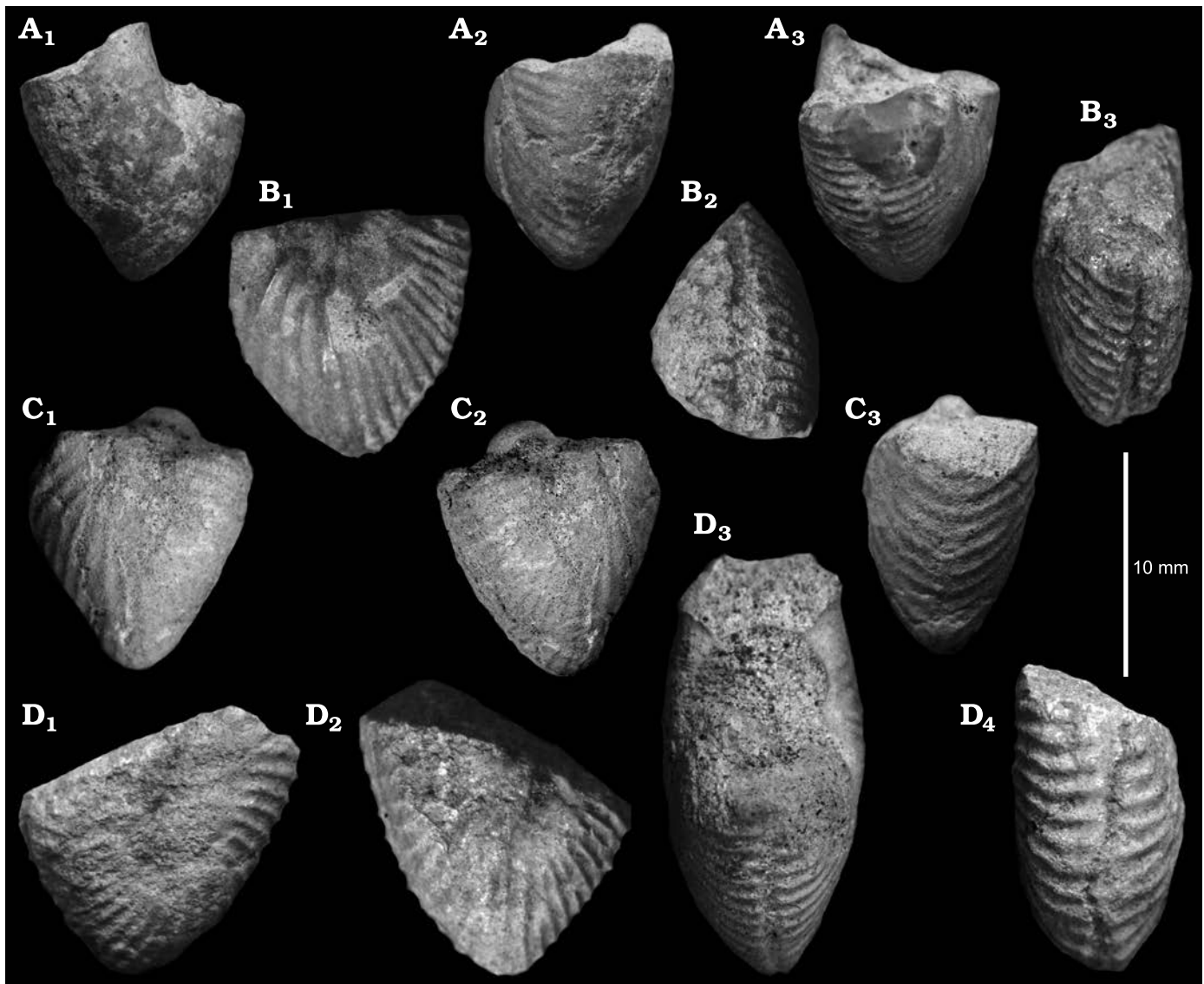


Fig. 6. Strigoceratid ammonoid *Oecoptychius refractus* (Reinecke, 1818) [m] from Ogradzieniec quarry, *Quenstedtoceras lamberti* Zone, upper Callovian. A. GIUS 8-3657/12 in lateral (A₁), dorsal (A₂), and dorsal (A₃, note the ribbing pattern) views. B. GIUS 8-3657/5 in lateral (B₁) and ventral (B₂, B₃, note the ribbing pattern) views. C. GIUS 8-3657/3 11 in lateral (C₁), opposite lateral (C₂), and ventral (C₃) views. D. GIUS 8-3657/4 in lateral (D₁), opposite lateral (D₂), and ventral (D₃, D₄, note the ribbing pattern) views.

1924 *Oecoptychius refractus* Haan; Roman and Debrun 1924: 106, pl. 11: 5.

1928 *Oecoptychius refractus* Haan; Sayn and Roman 1928: 150, pl. 10: 12.

1928 *Oecoptychius refractus* (Reinecke); Spath 1928: 278, pl. 81: 5.

1932 *Oecoptychius refractus* Reinecke; Corroy 1932: 120, pl. 10: 10–11.

1952 *Oecoptychius refractus* (Haan); Makowski 1952: 31, pl. 3: 3.

1958 *Oecoptychius refractus* Reinecke; Collignon 1958: 28, fig. 115.

1985 *Oecoptychius refractus* (Reinecke); Schlegelmilch 1985: 137, pl. 54: 4.

1987 *Oecoptychius refractus* (Reinecke); Callomon et al. 1987: 26, pl. 3: 7.

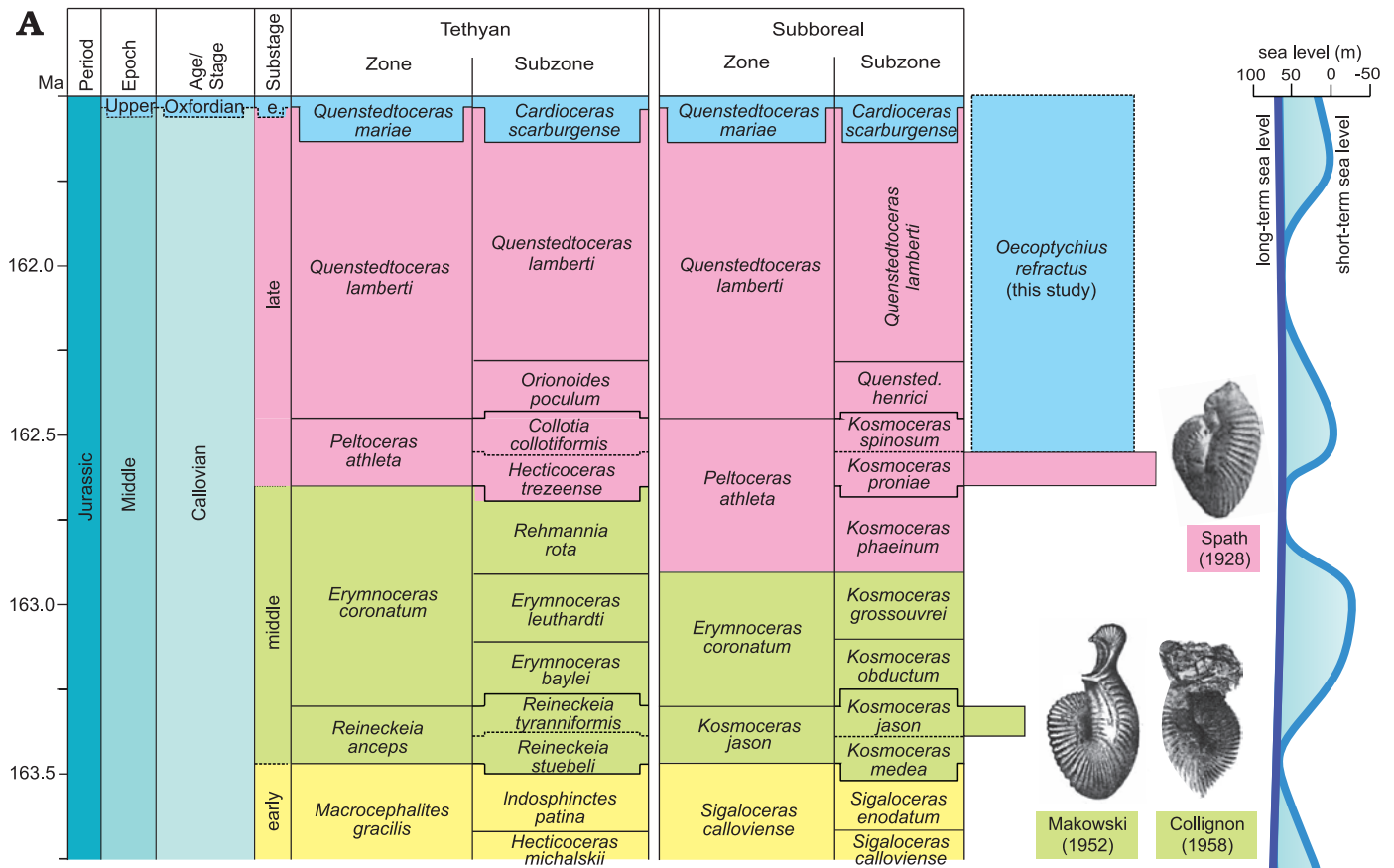
1994 *Oecoptychius refractus* (Reinecke); Fischer 1994: 153, pl. 60: 2.

1998 *Oecoptychius refractus* (Reinecke); Schweigert and Dietze 1998: pls. 6: 5, 8: 5, 9: 4–11.

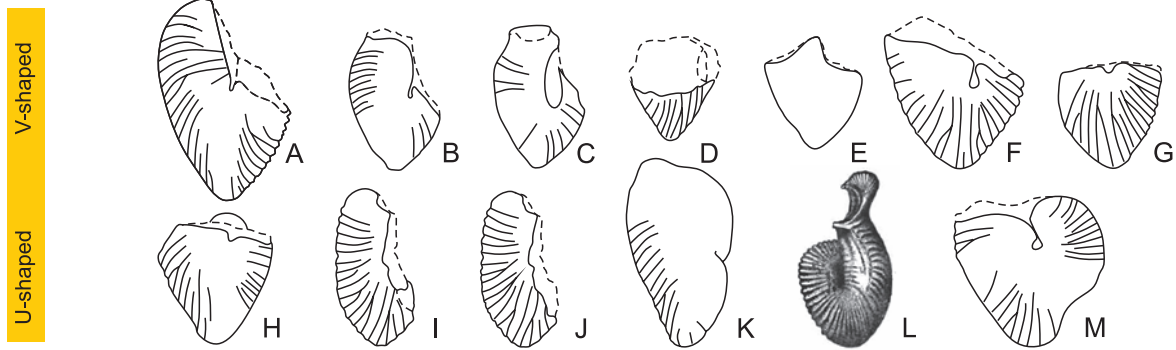
Type material: Lectotype: NMC 52/1, original of Reinecke (1818: fig. 29), designated by Zeiss in Heller and Zeiss (1972). Paralectotype: NMC 52/2, original of Reinecke (1818: fig. 27) (see Schweigert and Dietze 1998).

Type locality: Probably eastern Franconian Alb (area of Trockau) (for further details, see Schweigert and Dietze 1998).

Fig. 7. Biozonation and morphological variation in *Oecoptychius refractus* (Reinecke, 1818) [m]. A. Biozonation used in the present study with the occurrence of *O. refractus* (Reinecke, 1818) noted in Kachchh (western India; Spath 1928), Poland (Makowski 1952), and Madagascar (Collignon 1958). B. Morphological variation in *O. refractus* (Reinecke, 1818) [m]. A, GIUS 8-3657/9; B, GIUS 8-3657/9; C, GIUS 8-3657/8; D, GIUS 8-3657/6; E, GIUS 8-3657/12; F, GIUS 8-3657/4; G, GIUS 8-3657/5; H, GIUS 8-3657/3; I, GIUS 8-3657/11; J, GIUS 8-3657/10; K, GIUS 8-3657/7; L, specimen of Makowski (1952: 31, pl. 3: 3; no mention of specimen number); M, GIUS 8-3657/2; N to AD, SMNS 70655/1–17, respectively.



B *Oecoptychius refractus* (Reinecke, 1818)
Morphological variations recorded from the upper Callovian *Peltoceras athleta* Zone (Poland)



Oecoptychius refractus (Reinecke, 1818)
Morphological variations recorded from the middle Callovian *Kosmoceras jason* Zone (France; this study)

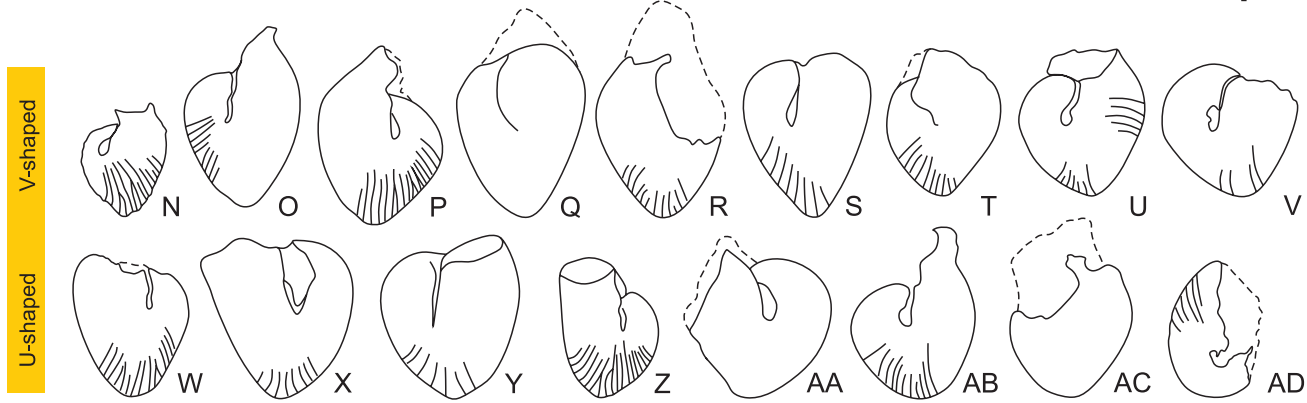




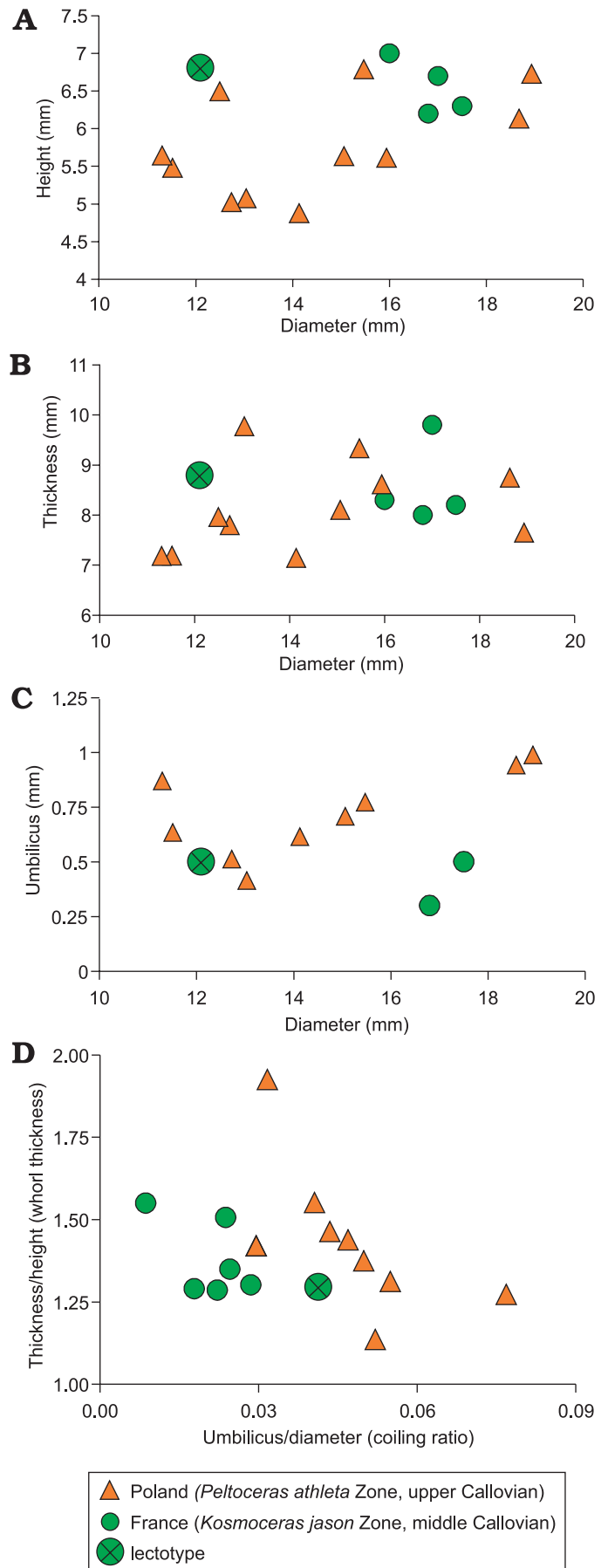
Fig. 8. Strigoceratid ammonoid *Oecoptychius refractus* (Reinecke, 1818) [m], SMNS 63457/1, from Ornatenton Formation, *Kosmoceras jason* Zone, Neidlingen, SW Germany, middle Callovian, Middle Jurassic. Note the strigations, a character noted only in well-preserved specimens and reminiscent of species attributed to *Phlyticeras polygonium* (Zieten, 1831) var. *wageni* [M] and considered herein to represent macroconch of *O. refractus* (Reinecke, 1818).

Type horizon: *Erymnoceras coronatum* Zone, middle Callovian, Middle Jurassic.

Measurements.—See Table 1.

Description.—The inner and the early part of the middle whorls not visible in any of the studied specimens. The middle and outer whorls are characterized by: (i) primaries long and sharp, bifurcate at mid- to outer third of whorl height into two forwardly inclined equally sharp secondaries, (ii) straight primaries arising from the rounded umbilical margin, (iii) with increasing shell diameter, the rounded umbilical region developing a smooth area; hence, with secondaries only visible at the outer third of whorl height, (iv) a distinct kink in the body-chamber, i.e., at larger shell sizes (on the phragmocone and in front of the body-chamber kink, in the case of a mold), a ventral groove (furrow) is noted, (v) morphological variation in the shape of the body-chamber with a gradation from V- to U-shape in longitudinal section (Fig. 7).

Fig. 9. Dimensional proportions of *Oecoptychius refractus* (Reinecke, 1818) [m]. The French and Polish specimens are compared with a reference point of the lectotype. A. Whorl height vs. shell diameter. B. Whorl thickness vs. shell diameter. C. Umbilicus vs. shell diameter. D. Whorl thickness vs. coiling ratio. For all given dimensional proportions, the French and Polish specimens form different groups.



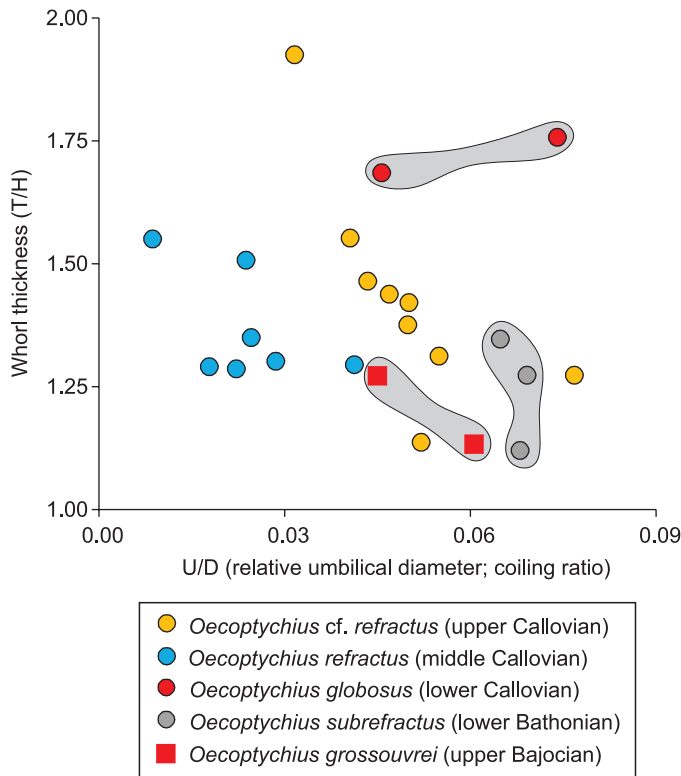


Fig. 10. Comparative dimensional proportions of various species of *Oecoptychius* Neumayr, 1878. Shaded areas display the range of variation in dimensional proportions.

In specimens preserved with the shell especially in the area of the body-chamber, and rarely on the phragmocone, a strigoceratid spiral striation is present (see Schweigert and Dietze 1998: pls. 6: 5; 9: 8, 9). A specimen with remains of the shell with striation, from the Ornatenton Formation (*Kosmoceras jason* Zone) of Neidlingen, SW Germany is illustrated (Fig. 8). Even if the shell is preserved, it often remains in the surrounding rock matrix and only the molds lacking the shell are collected. On molds, the spiral striae are occasionally discernible in large specimens; none of the present specimens ($D_{\max} = 21$ mm) preserve this feature. In rare cases when the shell is preserved, a smooth band is also observed which, like the furrow, disappears at the end of the body-chamber.

The upper Callovian specimens from Poland are more similar to the lectotype by means of the dimension parameters (more evolute and compressed; average U/D = 0.05; T/H = 1.44, respectively) and form a separate grouping when compared to the much larger middle Callovian French specimens (Fig. 9, Table 1). The whorl thickness versus coiling ratio also displays separate grouping (Fig. 9D, Table 1).

Remarks.—*Oecoptychius grossouvrei* Brasil, 1894 (*Parkinsonia* Zone, upper Bajocian, Middle Jurassic; see also Schweigert and Dietze 1998: 22, pl. 1: 3) is morphologically close to *Oecoptychius refractus* (Reinecke, 1818) described herein, but lacks the distinctive body-chamber kink, has a somewhat

oval-shaped body-chamber and finer secondaries restricted to the outer third of the whorl height.

Oecoptychius subrefractus (Buckman, 1920) (*Morphoceras macrescens* Subzone, *Zigzagiceras zigzag* Zone, lower Bathonian, Middle Jurassic; see also Dietl 1986; Dietze et al. 1997; Schweigert and Dietze 1998) has a similar but somewhat less developed body-chamber kink (Schweigert and Dietze 1998: 22, pl. 1: 3); it is also relatively compressed and evolute (Fig. 9, Table 1) and with a finer ornamentation.

Oecoptychius globosus Schweigert and Dietze, 1998 (*Proplanulites koenigi* Zone, lower Callovian; original of Quenstedt 1886: pl. 86: 51) is a very large form (27 mm shell diameter, Couffon 1919; see Table 1) but resembles *O. refractus* in having the mid-ventral furrow, primaries splitting into two ribs and the smooth umbilical region but lacks the characteristic and pronounced body-chamber kink; the mid-ventral furrow is less developed in *O. globosus* (see Schweigert and Dietze 1998: pl. 4: 6–7).

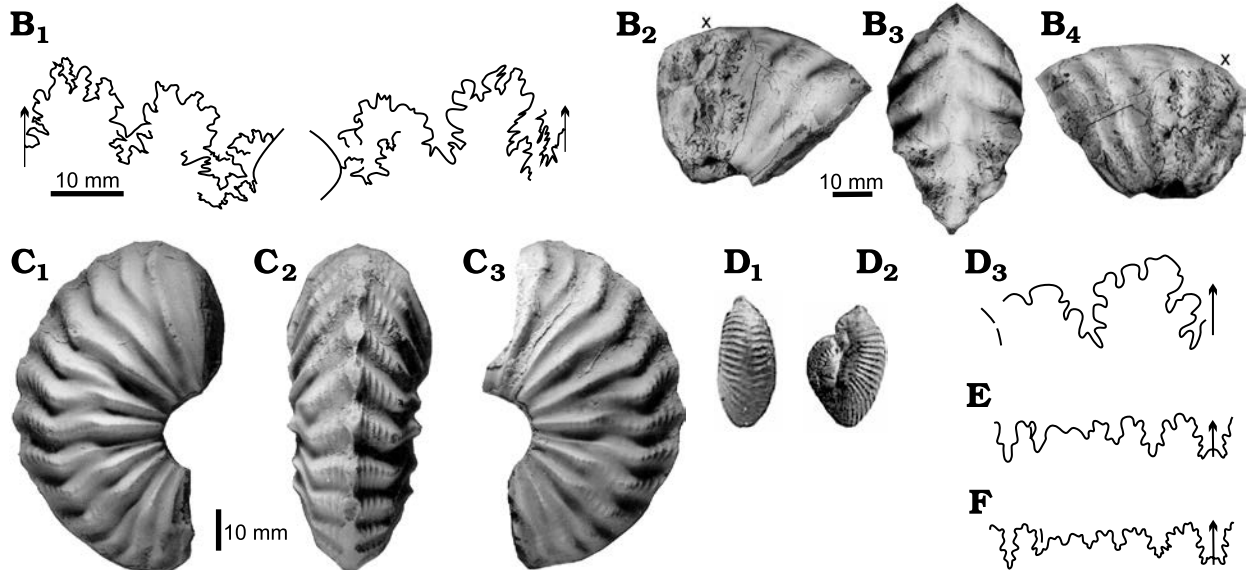
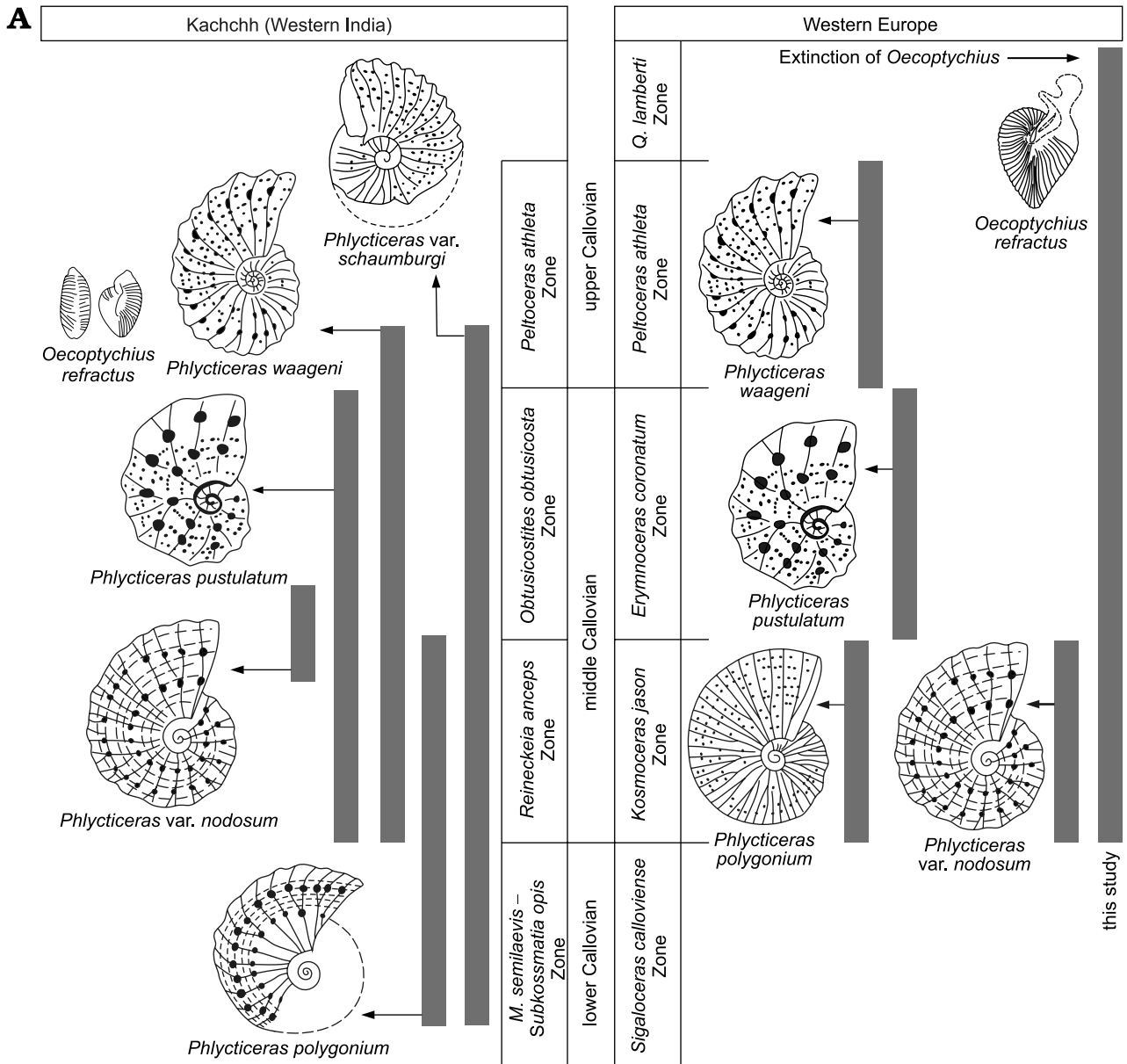
In terms of dimensional proportions (whorl thickness vs. coiling ratio; Fig. 10), the *O. grossouvrei* (*Parkinsonia parkinsoni* Zone, upper Bajocian) falls within the *O. refractus* range, whereas both the *O. subrefractus* (*Zigzagiceras zigzag* Zone, lower Bathonian) and *O. globosus* (*P. koenigi* Zone, lower Callovian) are outliers (Fig. 10) and morphologically quite different (Schweigert and Dietze 1998).

Stratigraphic and geographic range.—*Kosmoceras jason* Zone (middle Callovian) to *Quenstedtoceras lamberti* Zone (upper Callovian); Poland (middle and upper Callovian; the latter is from this study), Germany (middle Callovian), France (middle and upper Callovian), Madagascar (middle Callovian), Kachchh (upper Callovian).

Discussion

Morphological variation.—Schweigert and Dietze (1998), based largely on their data from southern Germany and France, noted that *Oecoptychius refractus* displays (i) a range of variation of adult size at the stage-level, and (ii) that the average shell size is reduced from the middle (*Kosmoceras jason* and *Erymnoceras coronatum* zones) to the upper Callovian (basal part of the *Peltoceras athleta* Zone). In the present study, based on a more comparative look at the middle and upper Callovian specimens (Fig. 7), three characteristic features of *O. refractus* are noted: (i) the changes in the body-chamber are gradational between V- to U-shape, (ii) there is no reduction in morphological variation (relative abundance of V- to U-shaped body-chambers) over time from middle to late Callovian, although forms with the V-shaped body-chamber do slightly dominate (53–54%), and (iii) there is indeed a general reduction in size (shell diameter) from the larger middle Callovian (average: 18.9 mm) to the smaller late Callovian (average: 14.6 mm) forms.

This illustrated morphological variation within the specimens of *O. refractus* from different localities and from dif-



ferent time intervals (Fig. 9) has a bearing on the widely applicable concept of morphology-based species assignments and reliability of these species and their varieties where there are no gradational forms. Here, we document a series of gradational forms of *O. refractus* that remains the same through time until its demise in the late Callovian (Fig. 9).

Dimorphic pairing.—Schweigert and Dietze (1998: 31, fig. 2) indicated the following dimorphic pairing: *Oecoptychius* cf. *refractus* [m]–*Phlycticeras polygonium* [M], *Oecoptychius refractus* [m]–*Phlycticeras pustulatum* [M] and *Oecoptychius* cf. *refractus* [m]–*Phlycticeras waageni* [M] (see also Schweigert et al. 2003). Here, based on the variation in *O. refractus* (Fig. 7), *O. refractus*, and *O. cf. refractus* of Schweigert and Dietze (1998) are considered as *O. refractus*.

Both in southern Germany and in western France, *O. refractus* [m] occurs in the beds of the *Kosmoceras jason* Zone (middle Callovian, Middle Jurassic), independent from different lithologies in both regions. In this zone, a highly variable *Phlycticeras polygonium* [M] is common, represented by almost smooth (var. *laevigatum* of Quenstedt 1887) to stronger ornamented variants (var. *suevicum* of Quenstedt 1887); most of them share a rather slender whorl section, but some of which (var. *nodosum* of Quenstedt 1887) are transitional to the stratigraphically younger and stronger ornamented *P. pustulatum* [M]. The co-occurrence and acme of *Phlycticeras polygonium* [M] and *Oecoptychius refractus* [m] in the *K. jason* Zone has contributed much to the recognition of the dimorphic pairing between these genera.

Spath (1928) noted the co-occurrence of *Phlycticeras waageni* [M] (*P. polygonium* var. *waageni* [M] of Jain 2017: fig. 13f–n) (see Fig. 11B–H) and *O. refractus* [m]. The suture line given by Spath (1928: pl. 81: 5c) (see Fig. 11I) resembles that of *P. polygonium* var. *waageni* [M] as illustrated by Jain (2017), and also the general ribbing pattern and the striation (see Fig. 11C–H). However, Schweigert and Dietze (1998: 22, fig. 1) considered the suture lines of their *O. refractus* [m]–*P. polygonium* [M] pair closer to *P. waageni* (see Fig. 11J, K). Jain (1997: figs. 2, 3) recorded the presence of *Phlycticeras* gr. *pustulatum* [M] in the middle Callovian of Jumara Dome (Kachchh, western India) (*Phlycticeras polygonium* [Zieten, 1831] var. *nodosum* [Quenstedt, 1887] [M]; see also Schweigert and Dietze 1998: 16). Based on this and

the presence of longitudinal striae in *O. refractus* (Fig. 8) these authors considered them as dimorphic pairs.

However, here, based on available data, *Phlycticeras polygonium* var. *waageni* [M] is considered as the dimorphic partner of *O. refractus* [m] (Fig. 11). This assignment is provisional, as the inner whorls of the var. *waageni* are not known, although, both dimorphs have similar stratigraphical ranges, from the base of the middle Callovian to the base of the upper Callovian (Fig. 11) (see also Jain 2017). These dimorphs have large differences in their shell diameters; the macroconch measures a maximum of 170 mm (Schweigert and Dietze 1998), whereas the microconch measures a maximum of 27 mm (Couffon 1919).

Palaeobiogeography.—Most records of *Oecoptychius refractus* (Reinecke, 1818) come from western Tethyan localities (Poland, Germany, and France) as compared to the eastern Tethyan ones (Madagascar and India). Possible reasons include (i) collecting bias due to much longer and more extensive sampling in France and Germany as compared to other areas where only random samples were picked up, (ii) collecting bias due to exposure availability in Europe, and (iii) an actual phenomenon explained by role of global eustasy; rising sea level (transgression) would result in more available niches (Fig. 7A; see also Haq 2018). Rising sea levels would have favored the formation of new niches and seaways to facilitate increased species distribution (Fig. 7A). However, only, more sampling can provide a conclusive answer.

Conclusions

Oecoptychius refractus (Reinecke, 1818) ranges from the *Kosmoceras jason* Zone (middle Callovian) to the *Quenstedtoceras lamberti* Zone (upper Callovian). The *Q. lamberti* Zone occurrence from southern Poland is probably the youngest record of this species worldwide. The two Kachchh (western India) specimens reported by Spath (1928) are assigned to the lower part of the upper Callovian *Peltoceras athleta* Zone; globally, this is now the second upper Callovian occurrence of *O. refractus*. Based on the present study, *O. refractus* is characterized by large morphological variation in the shape of the body-chamber, displaying

← Fig. 11. Relationship of *Phlycticeras* [M] Hyatt, 1900, with *Oecoptychius* Neumayr, 1878 [m]. **A.** Middle–upper Callovian occurrences of species of *Phlycticeras* [M] with their corresponding microconch, *Oecoptychius refractus* (Reinecke, 1818). **B, C.** *Phlycticeras polygonium* var. *waageni* Buckman, 1914, from Jara, 10 km north of Jumara, Kachchh, western India, middle Callovian (after Jain 2017). **B.** SJ/JA/99-00/23, suture line (B₁), lateral (B₂), ventral (B₃), and opposite lateral (B₄) views. **C.** Ju/B44/1, lateral (C₁), ventral (C₂), and opposite lateral (C₃) views. **D, E.** *Oecoptychius refractus* (Reinecke, 1818). **D.** G.S.I. No. 2/88 (Raj Nath collection) from Nurrah, Kachchh, western India, upper Callovian, ventral (D₁) and lateral (D₂) views, and suture line (after Spath 1928: 278, pl. 81: 5c) (D₃). **E.** Suture line after Schweigert and Dietze 1998. **F.** *Phlycticeras waageni* Buckman, 1914, suture line after Schweigert and Dietze 1998: 22, fig. 1b. **E, F.** based on the similarity of suture line and similar strigations (see Fig. 8), Schweigert and Dietze (1998) considered *Phlycticeras polygonium* (Zieten, 1831), *Phlycticeras pustulatum* (Reinecke, 1818), and *Phlycticeras waageni* Buckman, 1914, as the macroconch of *Oecoptychius refractus* (Reinecke, 1818) [m]. However, in this study, based on similarity of suture lines (B₁, D₃), morphological characteristics (B₂–B₄, C), and stratigraphic occurrences of *Oecoptychius refractus* (Reinecke, 1818) and *Phlycticeras polygonium* var. *waageni* (= *Phlycticeras waageni*), are considered as a dimorphic pair. See text for further explanation. **A, D–F,** not to scale. Abbreviations: *M.*, *Macrocephalites*; *Q.*, *Quenstedtoceras*. Stratigraphic ranges for Kachchh (Western India) are after Jain (2017) and for Western Europe are after Schweigert and Dietze (1998); x marks the end of the phragmocone stage.

a gradation from V- to U-shaped body-chamber. In terms of dimensional proportions, the smaller upper Callovian specimens from southern Poland are closer to the lectotype (more evolute and compressed) and also form a separate grouping as compared to the much larger middle Callovian specimens from western France. Additionally, *Phlycticeras polygonium* var. *waageni* [M] is considered here as the dimorphic partner of *O. refractus* [m]; both dimorphs have similar stratigraphic ranges, from the base of the middle Callovian to the base of the upper Callovian. The *O. refractus* samples are recorded dominantly from western Tethyan localities (Poland, Germany, and France) and less so from eastern Tethyan localities (Madagascar and India). However, more sampling is needed in the eastern Tethyan region to better understand the palaeobiogeographic distribution of *O. refractus* and its causal factors.

Authors' contributions

SJ carried out the study, participated in the conceptualization and drafted the manuscript. GS participated in drafting and reviewing the manuscript. MAS carried out the fieldwork, geological data collection, participated in the fossil preparation and measurements. BJP carried out part of the fieldwork. All authors read and approved the final manuscript.

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