SPP2 Journal Code | 1294 Manuscript No. | WILEY | Dispatch: 14.12.19 | No. of pages: 28 | CE: Geetha M | PE: Raymond Appavoo M.

[Papers in Palaeontology, 2019, pp. 1–28]

# COMPARATIVE CRYSTALLOGRAPHY SUGGESTS MANIRAPTORAN THEROPOD AFFINITIES FOR LATEST CRETACEOUS EUROPEAN ‘GECKOID’ EGGSHELL

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Typescript received 15 April 2019; revised 12 October 2019; accepted in revised form 31 October 2019

**Abstract:** Thin fossil eggshell from Upper Cretaceous deposits of Europe, characterized by nodular ornamentation similar to modern gekkotan eggshell, has mostly been interpreted as gekkotan (=‘geckoid’) in origin. However, in some cases, as for the oogenus *Pseudogeckoolithus*, a theropod affinity has also been suggested. The true affinity of these fossil geckoid eggshells has remained controversial due to the absence of analytical methods for identifying genuine gecko eggshell in the fossil record. In this study, we apply electron backscatter diffraction (EBSD) analysis to latest Cretaceous European geckoid (including *Pseudogeckoolithus*) eggshell, in comparison with modern gekkotan and theropod (avian) eggshell. We found that *Pseudogeckoolithus* has a definite theropod eggshell-like crystallographic configuration, in clear contrast to that seen in modern geckos. Furthermore, the crystallography of the nodular ornamentation in *Pseudogeckoolithus* is similar to that seen in megapode eggshell, but different from that of gecko eggshell, despite superficial morphological similarity. The remarkable morphological similarities between *Pseudogeckoolithus* and modern gecko eggshells are thus convergent, and the ‘gekkotan affinity’ hypothesis can be dismissed for *Pseudogeckoolithus*. This study provides a template for differentiating true gekkotan from dinosaurian eggshells in the fossil record. The potential functional significance of eggshell ornamentation, lost in most modern birds, requires further study, and experimental zoological approach may shed light on this issue. Finally, the present results suggest caution about the dangers of using potentially homoplastic eggshell characters in eggshell parataxonomy.

**Key words:** eggshell, electron backscatter diffraction, gecko, homoplasy, ornamentation, theropod.

FOSSIL eggs and eggshells provide a unique opportunity to study aspects of the reproductive biology of extinct amniotes (e.g. Tanaka *et al.* 2015, 2019; Varricchio & Jackson 2016; Amiot *et al.* 2017; Wiemann *et al.* 2018; Choi *et al.* 2019*a*). Among extant oviparous (egg-laying) amniotes, all archosaurs and some turtles lay rigid-shelled eggs, while the eggs of most lepidosaurs (squamates and rhynchocephalians) have a soft, leathery shell with a low degree of mineralization (Sander 2012; Skawiński & Tałanda 2014). Because soft eggshell has a low preservation potential (Hirsch 1996), almost all previously studied fossil eggshells have been found to belong to archosaurs or chelonians. Nevertheless, there are also a small number of fossil squamate eggshell reports in the literature (Choi *et al.* 2019*b*, table S1). These shells are very thin and share similarities in their ornamentation – and in some cases also in their microstructure – with eggshells of Gekkota (Squamata), the only extant lepidosaurian clade besides the Dibamidae, with some of its members laying rigid-shelled eggs (Sander 2012; Skawiński & Tałanda 2014), and with a fossil record dating back to the Early Cretaceous (Daza *et al.* 2014). Given that many maniraptoran (Dinosauria, Theropoda; a clade of bird-like theropods, including modern birds) eggshells are characterized by prismatic shell units (e.g. Mikhailov 1997*a*; Zelenitsky *et al.* 2002; Varricchio & Jackson 2004) and modern gekkotan eggshells have a similar-looking jagged columnar structure (Schleich & Kästle 1988; Packard & Hirsch

doi: 10.1002/spp2.1294

1989; Hirsch 1996; Mikhailov 1997*a*; Choi *et al.* 2018), the gekkotan or maniraptoran affinities of some fossil eggshells remained undecided. Thus, in the absence of *in ovo* embryos or at least body fossils in close association with the eggs or eggshells, there has been no rigorous way to test whether superficially gecko-like fossil eggshells are genuinely gekkotan or, in fact, archosaurian in origin.

Representative cases of fossil eggshell with such ambiguous identity were *Pseudogeckoolithus* and 'morphotype geckonoïde' (Vianey-Liaud & Lopez-Martinez 1997; Garcia 2000) described from the upper Upper Cretaceous (Campanian–Maastrichtian) continental deposits of western Europe. These eggshells are characterized by dispersituberculate ornamentation, which is very similar to that of *Gekko gecko* (Gekkota) eggshell (Schleich & Kästle 1988; Packard & Hirsch 1989; Choi *et al.* 2018). According to Vianey-Liaud & Lopez-Martinez (1997), *Pseudogeckoolithus*, as its name implies, is macroscopically similar to gecko eggshell, but its micro- and ultrastructural features were identified as a 'dinosauroid prismatic type', thus arguing for a dinosaurian origin. However, Garcia (2000) also reported gecko-like eggshells that are morphologically reminiscent of *Pseudogeckoolithus* but which she nevertheless referred to as morphotype geckonoïde, pointing out their microstructural similarity with extant gekkotan eggshell. Moreover, Sellés (2012) argued that even *Pseudogeckoolithus* lacks a mammillary layer and is merely composed of irregular prisms, hence, it is not of dinosaurian origin, but represents instead a Mesozoic lizard eggshell. Accordingly, European Late Cretaceous eggshells, which are very similar to either *Pseudogeckoolithus* or 'geckonoïde' eggshells, have been usually associated with Gekkota (e.g. Garcia & Vianey-Liaud 2001; Csiki-Sava *et al.* 2015, 2016; Botfalvai *et al.* 2017). In contrast, Prondvai *et al.* (2017) concluded recently that the most abundant fossil eggshells ('morphotype I' or 'MT I') from the Santonian of Iharkút, Hungary, which resemble both *Pseudogeckoolithus* and the French 'geckonoïde' morphotype, have a theropod affinity based on the presence of a mammillary layer, in agreement with Vianey-Liaud & Lopez-Martinez (1997). Furthermore, Prondvai *et al.* (2017) suggested that, along with the Hungarian MT I eggshells, putative 'gecko-like' eggshells from the Upper Cretaceous deposits in Romania, Spain and France might have theropod affinities as well, consistent with the interpretation of North American dispersituberculate eggshells (e.g. Zelenitsky *et al.* 1996; Jackson & Varricchio 2010, 2016; Table 1). These conflicting views on the nature of the Late Cretaceous geckoid eggshells can only be resolved with a diagnostic methodology that allows identification of genuine gekkotan eggshells in the fossil record.

Using electron backscatter diffraction (EBSD) analysis, Choi *et al.* (2018) showed that crystallographic configuration of extant gekkotan eggshell is fundamentally different from that of dinosaurian (including avian) eggshell (see Choi *et al.* 2019*a*, table 1). Hence, EBSD is adequate for differentiating gekkotan from theropod eggshell in the fossil record. Here, we apply EBSD analysis to different geckoid eggshell samples recovered from European Upper Cretaceous deposits in order to test their putative gekkotan affinity by comparing them with diverse sauropsid eggshells including those of extant Gekkota and Aves. During our study, we identified several distinct construction pathways of nodular eggshell ornamentation, and the parataxonomic importance of these is also discussed.

## GEOLOGICAL AND PALAEOGEOGRAPHICAL SETTING

Vertebrate-bearing Upper Cretaceous (Santonian–Maastrichtian) continental beds are distributed discontinuously across a wide area in Europe (Csiki-Sava *et al.* 2015; Fig. 1A). These deposits were laid down in marginal marine, coastal plain or inland fluvial settings in an archipelago on the northern margin of the Neotethyan area. Although most of these former 'islands' yielded only few fragmentary fossils, some of them hosted a wide variety of vertebrate taxa. The most important of these is 'Bakony Island' in present-day western Hungary (with the Santonian Iharkút locality; Ősi *et al.* 2012; Botfalvai *et al.* 2016); 'Hațeg Island' in what is central-western Romania (with a number of localities ranging in age from the latest Campanian to the late Maastrichtian; Csiki-Sava *et al.* 2016); and the much larger 'Ibero-Armorican Landmass' covering the Iberian Peninsula and the southern part of present-day France (with numerous localities spanning the early Campanian – latest Maastrichtian time interval; e.g. Vila *et al.* 2016; Fondevilla *et al.* 2019). All three areas have yielded, besides diverse vertebrate remains, geckoid eggshells (Figs 1A, 2). We will review here briefly the general geological setting for these areas, as well as the geology and fossil content of the localities that yielded specimens used in the present study (for more details, see Choi *et al.* 2019*b*, texts S1, S2).

### *Santonian of Iharkút, Hungary*

In Hungary, subaerially exposed fossiliferous Upper Cretaceous continental deposits are restricted to the Bakony region (Fig. 2A). These are grouped into two laterally interdigitating units: the mainly fluvial Csehbánya Formation, and the Ajka Coal Formation, deposited in coastal plain swamps (e.g. Haas *et al.* 1992; Botfalvai *et al.* 2016). These are represented by a variety of siliciclastic rocks, ranging from coarse conglomerates to marls and

**TABLE 1.** List of ootaxa characterized by dispersituberculate ornamentation.

| Continent | Oogenus | Oospecies | Shell thickness (mm)† | ML:CL | Ornamentation | Reference |
|---|---|---|---|---|---|---|
| Europe | *Prismatoolithus* | *P. tenuis* | 0.3–0.6 | 1:5.67 | Smooth to dispersituberculate | Vianey-Liaud & Crochet (1993); Vianey-Liaud & Lopez-Martinez (1997) |
| | | *P. trempii* | 0.25–0.53 | 1:4–1:5 | Smooth to dispersituberculate | Sellés *et al.* (2014) |
| | | *P. caboti* | 0.5–0.6 | 1:7–1:9 | Dispersituberculate | Garcia *et al.* (2000) |
| | *Pseudogeckoolithus* | *P. nodosus* | 0.30; 0.35 | 1:7–1:9 | Dispersituberculate | Vianey-Liaud & Lopez-Martinez (1997) |
| | *Pseudogeckoolithus* | Iharkút (A) | 0.151; 0.192 | 1:5–1:6 | Dispersituberculate | Prondvai *et al.* (2017) |
| | *Pseudogeckoolithus* | Petresti black lens (B) | 0.199; 0.251 | 1:5–1:6 | Dispersituberculate | Present study |
| | *Pseudogeckoolithus* | Valioara Fantanele (C) | 0.223; 0.294 | 1:8–1:9 | Dispersituberculate | Present study |
| | *Pseudogeckoolithus* | Pui Classic (D) | 0.169; 0.208 | 1:1–1:2 | Dispersituberculate | Present study |
| | *Pseudogeckoolithus* | Blasi 2 (E) | 0.269; 0.338 | 1:3–1:4 | Dispersituberculate | Present study |
| Africa | *Pseudogeckoolithus* | *P. tirboulensis* | 0.13–0.29; 0.22–0.36 | 1:1–1:2 | Dispersituburculate | Vianey-Liaud & Garcia (2003); Garcia *et al.* (2003) |
| | *Tipoolithus* | *T. achloujensis* | 0.40–0.65 | 1:1–1:2 | Dispersituburculate | Garcia *et al.* (2003); Vianey-Liaud & Garcia (2003) |
| North America | *Porituberoolithus* | *P. warnerensis* | 0.45–0.78 | 1:1–1:2 | Dispersituberculate | Zelenitsky *et al.* (1996, 2017*a*, *b*); Zelenitsky & Sloboda (2005); Welsh & Sankey (2008); Tanaka *et al.* (2011); Oser (2018) |
| | *Continuoolithus* | *C. canadensis* | 0.65–1.28 | 1:4–1:11 | Dispersituberculate; ridges | Hirsch & Quinn (1990); Bray (1999); Zelenitsky *et al.* (1996, 2017*a*, *b*); Zelenitsky & Sloboda (2005); Tanaka *et al.* (2011); Jackson & Varricchio (2010); Jackson *et al.* (2015); Voris *et al.* (2018); Oser (2018) |
| | *Tristraguloolithus* | *T. cracioides* | 0.32–0.36 | 1:1.5 | Dispersituberculate | Zelenitsky *et al.* (1996) |
| | *Dispersituberoolithus* | *D. exilis* | 0.26–0.28 | 1:2.5 | Dispersituberculate | Zelenitsky *et al.* (1996) |
| | *Triprismatoolithus* | *T. stephensi* | 0.525–0.850 | 1:5 | Dispersituberculate | Jackson & Varricchio (2010); Zelenitsky *et al.* (2017*b*) |
| | *Tubercuoolithus* | *T. tetonensis* | 0.831–1.186 | 1:3 | Dispersituberculate; anastomotuberculate | Jackson & Varricchio (2010) |
| | *Dimorphoolithus* | *D. bennetti* | 0.561–0.850 | 1:2.6–1:3 | Dispersituberculate | Jackson & Varricchio (2016) |
| | ‘*Stillatuberoolithus*’ | ‘*S. storrsi*’ | 0.31–0.59 | 1:1.1–1:1.5 | Dispersituberculate | Oser (2018) |
| | *Macroelongatoolithus* | *M. carlylei* | 1.38–4.75 | 1:2–1:8 | Dispersituberculate; lineartuberculate | Simon *et al.* (2019) |

(continued)

**TABLE 1.** (Continued)

| Continent | Oogenus | Oospecies | Shell thickness (mm)† | ML:CL | Ornamentation | Reference |
|---|---|---|---|---|---|---|
| Asia | *Subtiliolithus* | *S. kachchhensis* | 0.35–0.45 | 1:1–1:2 | Dispersituberculate | Khosla & Sahni (1995); see also Sahni *et al.* (1994, fig. 13.10) |
| | | *S. microtuberculatus* | 0.3–0.4 | 3:1–2:1 | Dispersituberculate | Mikhailov (1991, 1997*a*, 2000) |
| | *Macroelongatoolithus* | *M. carlylei* | 1.38–4.75 | 1:2–1:8 | Dispersituberculate; lineartuberculate | Simon *et al.* (2019) |
| Eggshell fossils outside parataxonomy | | | | | | |
| South America | Type 3 Ratite morphotype | | 0.82–1.14 | ? | Dispersituberculate | Vianey-Liaud *et al.* (1997) |
| | Type 4 Ratite morphotype | | 0.50–0.64 | ? | Dispersituberculate | Vianey-Liaud *et al.* (1997) |
| Asia | Confirmed Enantiornithes egg | | 0.183–0.184 | 1:2 | Dispersituberculate? | Balanoff *et al.* (2008); Varricchio *et al.* (2015) |
| | Prismatoolithidae indet. | | 0.22–0.32 | 1:1–1:1.3 | Dispersituberculate | Tanaka *et al.* (2016) |

†XXXXX. CL, continuous layer; ML, mammillary layer.

claystones. Minor coaly interbeds are present in the Csehbánya deposits, but are common in the Ajka beds. Their Santonian age (Fig. 1B) is based mainly on palynostratigraphy (e.g. Bodor & Baranyi 2012) as well as on the biostratigraphically constrained latest Santonian–Campanian age of the overlying marine deposits (e.g. Haas 1983).

The most important fossils, representing a wide variety of vertebrate taxa (see Choi *et al.* 2019*b*, texts S1, S2), come from the Iharkút abandoned open-pit bauxite mine in the Csehbánya Formation (e.g. Ősi *et al.* 2012; Botfalvai *et al.* 2015). The vertebrate skeletal remains are occasionally associated with exclusively thin eggshell fragments (Botfalvai *et al.* 2015), among which Prondvai *et al.* (2017) identified different types of crocodyloid and theropod (including bird) eggshells, alongside a single fragment that was assigned to a squamate. *Pseudogeckoolithus* eggshell (see below, Systematic Palaeontology) is by far the most common, and the affinity was tentatively linked by Prondvai *et al.* (2017) to small-bodied theropods. These eggshells (named MT I morphotype in Prondvai *et al.* 2017 but here referred to *Pseudogeckoolithus*) occur in two different localities at Iharkút (e.g. Botfalvai *et al.* 2015): SZ-6, the main fossiliferous horizon, and SZ-7-8 (a pond deposit in a poorly drained floodplain; Botfalvai *et al.* 2016). The lithology at locality SZ-6 is interpreted as a flash-flood deposit within a fluvial channel, followed by slow infilling (Botfalvai *et al.* 2016). This locality (a high-diversity multitaxic macrovertebrate bonebed; Botfalvai *et al.* 2015) yielded the largest part of the vertebrates documented at Iharkút (see Choi *et al.* 2019*b*, text S2).

### *Uppermost Campanian–Maastrichtian of Transylvania, Romania*

Upper Cretaceous continental beds are widespread but occur patchily in western Romania, most importantly in the Haţeg Basin (Figs 1A, 2B). The litho- and chronostratigraphy, as well as the fossil content of these deposits, were recently reviewed by Csiki-Sava *et al.* (2015), and are briefly synthesized here. The continental beds are largely siliciclastic, ranging from coarse conglomerates to siltstones and mudstones. Locally, igneous products are also present within the successions, whereas other rock types are rare, except the Rusca Montană Basin where coal intercalations are known. Deposition took place in fluvially dominated environments, under a seasonally variable, dominantly semi-arid climate. The latest Campanian–Maastrichtian age of these deposits is constrained by biostratigraphically dated underlying marine beds (Melinte-Dobrinescu 2010; Vremir *et al.* 2014), and is corroborated by radiometric aging (Bojar *et al.* 2011), palynostratigraphy (Antonescu *et al.* 1983; Van Itterbeeck *et al.* 2005) and magnetostratigraphy (Panaiotu & Panaiotu 2010).

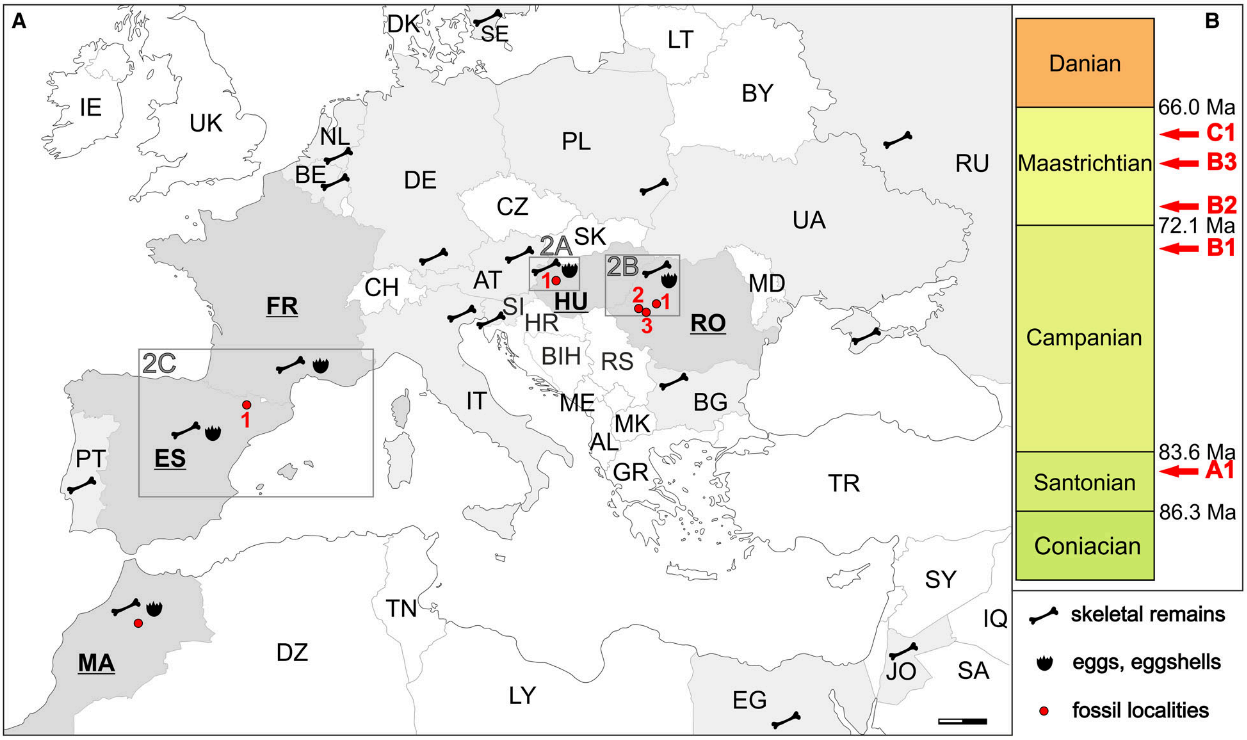


**FIG. 1.** Latest Cretaceous continental vertebrate distribution in the peri-Mediterranean area, with selected *Pseudogeckoolithus* localities (for more detail, see Fig. 2 and Choi *et al.* 2019*b*, texts S1, S2). A, outline map marking countries with latest Cretaceous continental vertebrate remains (highlighted in light grey), eventually associated with eggshells (dark grey). Distribution map based on Garcia *et al.* (2003), Weishampel *et al.* (2004), Chassagne-Manoukian *et al.* (2013), Csiki-Sava *et al.* (2015), Sallam *et al.* (2016, 2018), and Longrich *et al.* (2017). Standardized country abbreviations follow the ISO alpha-2 system (https://www.iso.org/iso-3166-country-codes.html). Boxes highlight the geographical position of the *Pseudogeckoolithus* fossil localities discussed in this paper, as well as the type locality of the Moroccan *Pseudogeckoolithus tirboulensis* (Vianey-Liaud & Garcia 2003; Achlouj 2 locality). Boxes 2A, Santonian locality SZ-6 in Iharkút (A1), western Hungary (former ‘Bakony Island’); 2B, latest Campanian–Maastrichtian localities Petreşti-Black Lens (B1), Vălioara-Fântânele (B2) and Pui-Classic (B3), in western Romania (former ‘Haţeg Island’); and 2C, late Maastrichtian locality Blasi 2 (C1), in southern France–central-northern Spain (former ‘Ibero-Armorican Landmass’). B, approximate stratigraphic position of the sampled *Pseudogeckoolithus* localities. A1–C1 denote fossil localities according to their respective boxes (A–C in A). Scale bar represents 200 km.

A rich assemblage of continental organisms is known from these deposits, including invertebrates, plants and vertebrates, the latter – best represented in the Haţeg Basin (Fig. 2B-e) – known for the dwarf dinosaurs (Benton *et al.* 2010; Csiki-Sava *et al.* 2015; Choi *et al.* 2019*b*, texts S1, S2). The vertebrate skeletal remains are sometimes associated with eggs and eggshell fragments. Besides megaloolithids of a contentious affinity (e.g. Grigorescu *et al.* 2010; Grellet-Tinner *et al.* 2012; Botfalvai *et al.* 2017), diverse thin eggshells are also present, but have remained mainly unstudied (Codrea *et al.* 2002; Csiki-Sava *et al.* 2008; Dyke *et al.* 2012), with the exception of a peculiar mixed assemblage of avian, crocodyloid and gekkotan eggshells (Fernández *et al.* 2019). Of these thin eggshells, the most commonly occurring ones belong to *Pseudogeckoolithus* (e.g. Codrea *et al.* 2010*a*; Vremir *et al.* 2015*a*; see below, Systematic Palaeontology), although frequently they were only referred to as geckoid or geckonoid (e.g. Codrea *et al.* 2002; Csiki-Sava *et al.* 2008, 2016). Three new *Pseudogeckoolithus* occurrences – one from the southwestern Transylvanian Basin and two from the Haţeg Basin – are reported here for the first time (Figs 1, 2B), and are described briefly in ascending order of age (see also Choi *et al.* 2019*b*, text S2).

The oldest locality is the Petreşti-Black Lens microvertebrate bonebed (MvBB) in the Transylvanian Basin (Figs 1, 2B) from the Petreşti–Arini section (Codrea *et al.* 2010*a*; Vremir 2010), a unique marine-to-continental transitional sequence spanning the latest Campanian – earliest Maastrichtian interval (e.g. Vremir *et al.* 2014); the recently identified Black Lens MvBB is probably latest Campanian in age (Vremir *et al.* 2015*b*). The MvBB is a poorly drained coastal plain deposit that yielded a rich assemblage of aquatic and terrestrial

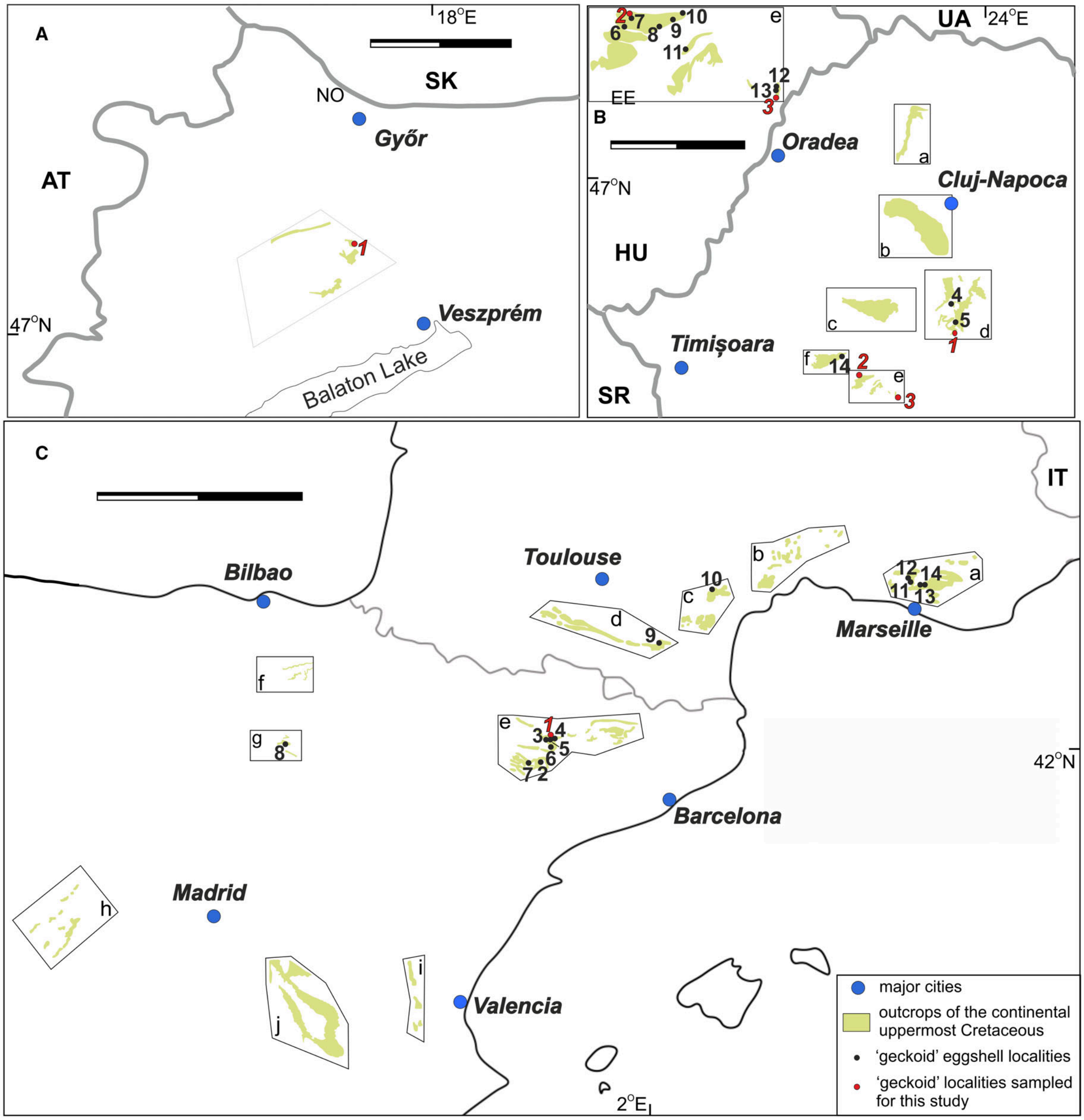


**FIG. 2.** Distribution of 'geckoid' (including both *Pseudogeckoolithus* and morphotype geckonoïde) eggshell-bearing localities in the uppermost Cretaceous (Santonian–Maastrichtian) of southern Europe (see Fig. 1), overlain on the approximate areal distribution of the main uppermost Cretaceous continental deposit outcrops (based on Haas *et al.* 1992; Pol *et al.* 1992; Ortega *et al.* 2015; Csiki-Sava *et al.* 2016; Corral *et al.* 2016; Pérez-García *et al.* 2016; Vila *et al.* 2016). A, Santonian, Hungary: 1, Iharkút localities Sz-6 and Sz 7-8 (Ősi *et al.* 2012; Botfalvai *et al.* 2016). B, uppermost Campanian–Maastrichtian, Romania: a, northwestern Transylvanian Basin; b, western Transylvanian Basin; c, Southern Apuseni Mountains; d, southwestern Transylvanian Basin; e, Haţeg Basin (also shown as enlarged inset); and f, Rusca Montană Basin. Localities: 1, Petreşti-Black Lens (present study); 2, Vălioara-Fântânele (present study); 3, Pui-Classic (present study); 4, Oarda de Jos A (Codrea *et al.* 2010*a*, *b*, *c*; Vremir 2010; Vremir *et al.* 2015*a*); 5, Sebeş-Glod (Vremir *et al.* 2015*a*); 6, Ciula Mică (Vasile 2010); 7, Budurone (Csiki-Sava *et al.* 2008); 8, Tuştea (Botfalvai *et al.* 2017); 9, General Berthelot BG-1 (Vasile *et al.* 2011*a*); 10, Crăguiş (Vasile *et al.* 2011*b*); 11, Toteşti (Codrea *et al.* 2002); 12, Pui Swamp (Voicu *et al.* 2018); 13, Pui Islaz (Garcia *et al.* 2002); 14, Fărcădeana (Vasile & Csiki-Sava 2011; Vasile *et al.* 2012; Csiki-Sava *et al.* 2016). C, Campanian–Maastrichtian, southern France and north-central Spain: a, Arc Basin; b, Hérault; c, Corbières-Haute Valley of Aude; d, Plantaurel-Haute Garonne; e, Southern Pyrenean Foredeep; f, Basque Country–Laño; g, Burgos Province; h, Segovia Province; i, Valencia area; j, Cuenca Province. Localities: 1, Blasi 2 (present study); 2, Fontllonga 6 (Vianey-Liaud & Lopez-Martinez 1997); 3, Serrat del Pelleu (Sellés 2012); 4, Molí del Baró (Sellés 2012); 5, Serrant del Rostià (Sellés 2012); 6, Camí del Soldat (Sellés 2012); 7, L'Espinau (Sellés 2012); 8, Quintanilla del Coco (Garcia 2000); 9, Rennes-le-Chateau (Cousin 1997); 10, Cruzy (Garcia 2000); 11, Vitrolles-Couperigne (Garcia 2000); 12, Vitrolles-La-Plaine (Valentin *et al.* 2012); 13, Trets (Kerourio 1982); 14, Le Neuve (Garcia 2000). Scale bars represent 50 km (A); 100 km (B); 200 km (C).

vertebrates (Vremir *et al.* 2015*b*), besides eggshell fragments, gastropods and charred wood remains.

In the Haţeg Basin, the chronostratigraphically older locality is the early Maastrichtian Vălioara-Fântânele locality (Figs 1, 2B; Grigorescu *et al.* 1999; Csiki-Sava *et al.* 2016). It was formed in a small depression with ponded, oxygen-poor waters, developed within the confines of a braided river floodplain (Vasile & Csiki-Sava 2010). The fossil accumulation is a classical MvBB with a rich and diverse vertebrate assemblage (Csiki-Sava *et al.* 2016; Choi *et al.* 2019*b*, text S2). These are associated with invertebrates and eggshells, including common geckoid (= *Pseudogeckoolithus*; see Systematic Palaeontology) ones.

The third, and geologically youngest, Romanian locality surveyed in the present study (Pui-Classic; Figs 1, 2B) is located near Pui; it is most probably late (although probably not latest) Maastrichtian in age (Csiki-Sava *et al.* 2016; Choi *et al.* 2019*b*, text S2). The fossiliferous bed formed in a well-drained floodplain setting, and represents a typical MvBB dominated by shed archosaur teeth, associated with other organic remains including common geckoid eggshells.

### *Campanian–Maastrichtian of northern Spain and southern France*

Upper Cretaceous continental and transitional deposits are widespread in central and northern Spain (most importantly in the Southern Pyrenean Foredeep, where they are represented by the Arén and Tremp formations: red and grey marls and clays, sandstones with local limestone levels; Mey *et al.* 1968), as well as in southern France (e.g. Csiki-Sava *et al.* 2015) (Figs 1, 2C). These deposits represent the lowermost Campanian – uppermost Maastrichtian interval in southern France, and the Campanian – uppermost 8 Maastrichtian in Spain, and are usually divided into local chronostratigraphic units that are often difficult to correlate with the standard chronostratigraphic divisions (e.g. Cojan & Moreau 2006; Csiki-Sava *et al.* 2015). Given that the Pyrenean area includes K–Pg boundary continental outcrops, a large number of magnetostratigraphic and biostratigraphic studies have been carried out in recent years, resulting in a detailed, although somewhat controversial, chronostratigraphic framework for the uppermost Cretaceous continental deposits (Fondevilla *et al.* 2016, 2019; Puértolas-Pascual *et al.* 2018).

The continental uppermost Cretaceous of Ibero-Armorica has yielded an important and diverse tetrapod fauna, including clutches, eggs and nests of several species of dinosaurs and crocodyliforms (Csiki-Sava *et al.* 2015; Sellés & Vila 2015; Canudo *et al.* 2016 and references therein). Most importantly, the oogenus *Pseudogeckoolithus* itself was erected from the early Maastrichtian aged Fontllonga 6 locality, within the Southern Pyrenean Foredeep (Vianey-Liaud & Lopez-Martinez 1997; Fig. 2C), and was subsequently identified in several other localities across the Southern Pyrenees (e.g. Sellés 2012) that span the early – late Maastrichtian interval (Fondevilla *et al.* 2016, 2019), 9 including the late Maastrichtian Blasi 2 locality (Pereda-Suberbioloa *et al.* 2009; Moreno-Azanza *et al.* 2014*a*). Furthermore, *Pseudogeckoolithus* or geckoid eggshells (often identified as morphotype geckonoïde by Garcia 2000) were also reported from the Maastrichtian Spanish Quintanilla del Coco locality (Fig. 2C; Pol *et al.* 1992), as well as from several localities spread across southern France (e.g. Kerourio 1982; Cousin 1997; Garcia 2000; Valentin *et al.* 2012; Fig. 2C).

Materials included in this study come from the Blasi 2 locality, an MvBB located on the northern flank of the Tremp Syncline (Southern Pyrenean Foredeep; Figs 1, 2C). It yielded a diverse vertebrate assemblage (López-Martínez *et al.* 2001; Blain *et al.* 2010; Torices *et al.* 2015) besides eggshell fragments (Moreno-Azanza *et al.* 2014*a*), including geckoid (*Pseudogeckoolithus,* see below, Systematic Palaeontology) eggshells as well.

## MATERIAL AND METHOD

### Late Cretaceous *Pseudogeckoolithus*

The most characteristic feature of the oogenus *Pseudogeckoolithus*, erected by Vianey-Liaud & Lopez-Martinez (1997) based on six eggshell fragments collected from the early Maastrichtian (magnetochron C31N) Fontllonga-6 locality (Lleida Province, Spain), is its dispersituberculate ornamentation. Although the holotype fragments are seemingly lost, this oogenus has been identified in several other localities across Ibero-Armorica (see review in Choi *et al.* 2019*b*, text S2; Fig. 2), as well as in northern Africa (Morocco; Vianey-Liaud & Garcia 2003; Fig. 1). On its turn, the geckonoïde eggshell type described by Garcia 10 (2000) is also very similar to *Pseudogeckoolithus* and may well be synonymous with this oogenus.

For this study, eggshell fragments showing dispersituberculate ornamentation almost identical to that of *Pseudogeckoolithus* and of the dinosaur prismatic morphotype were selected from three main European regions with important uppermost Cretaceous continental outcrops (Hungary, Romania and Spain; Csiki-Sava *et al.* 2015) (Figs 1–3; Choi *et al.* 2019*b*, text S2). Although unfortunately we could not access French geckonoïde material (e.g. Garcia 2000) for our analysis, hereafter, we collectively refer to all dispersituberculate European eggshells, including *Pseudogeckoolithus*, the unavailable French geckonoïde type and our eggshell samples, as ‘geckoid’ (between single quotation marks to avoid confusion with the Geckoid basic type and morphotype of

Mikhailov 1997*a*). Furthermore, despite their relatively diverse appearance (Table 1), all dispersituberculate eggshells included in this study are relatively thin (<350 μm, including ornamentation) and show pore openings at the top of some of the ornamental nodes (Fig. 3), which are further diagnostic features of the oogenus *Pseudogeckoolithus*.

From the specimens included in this study, the ‘geckoid’ eggshells from the Romanian locality of Vălioara-Fântânele and the Spanish locality of Blasi 2 (Fig. 3C, E) are thicker and have less dense ornamentation than specimens from the Hungarian locality of Iharkút and the Romanian localities of Petrești-Black Lens and Pui-Classic (Fig. 3A, B, D). Therefore, the former specimens are referred to as *Pseudogeckoolithus* cf. *nodosus* (Vianey-Liaud & Lopez-Martinez 1997), whereas the latter as *Pseudogeckoolithus* aff. *tirboulensis* (Vianey-Liaud & Garcia 2003) (see below, Systematic Palaeontology).

*Institutional abbreviations.* LPB [FGGUB], Laboratory of Paleontology, Faculty of Geology and Geophysics, University of Bucharest, Bucharest, Romania; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain (Canudo 2018); MTM, Hungarian Natural History Museum, Budapest, Hungary.

### *Fossil comparative materials*

In order to narrow down the possible dinosaurian taxonomic affinities of *Pseudogeckoolithus*, EBSD images of several types of dinosaur fossil eggshells were analysed and compared with Late Cretaceous *Pseudogeckoolithus*. These include hadrosaur (cf. *Maiasaura*), sauropod (*Megaloolithus* cf. *siruguei*), troodontid (*Prismatoolithus levis*) and enantiornithine (*Gobioolithus minor*) eggshells. The EBSD images of the hadrosaur and sauropod eggshells were already presented in Moreno-Azanza *et al.* (2013) and Moreno-Azanza *et al.* (2016), respectively. Although the sauropod eggshell example discussed in Moreno-Azanza *et al.* (2016) shows sufficiently well the overall crystallography of a typical sauropod eggshell, it was nonetheless significantly altered by taphonomic effects, thus we recommend to inspect the EBSD image of a well-preserved sauropod eggshell figured in Grellet-Tinner *et al.* (2011) and Eagle *et al.* (2015) as well. The EBSD images of the troodontid and enantiornithine eggshells are provided as representatives of confirmed maniraptoran eggshells; only brief accounts of these two maniraptoran eggshell types are provided here, given that a detailed description was given in Choi *et al.* (2019*a*).

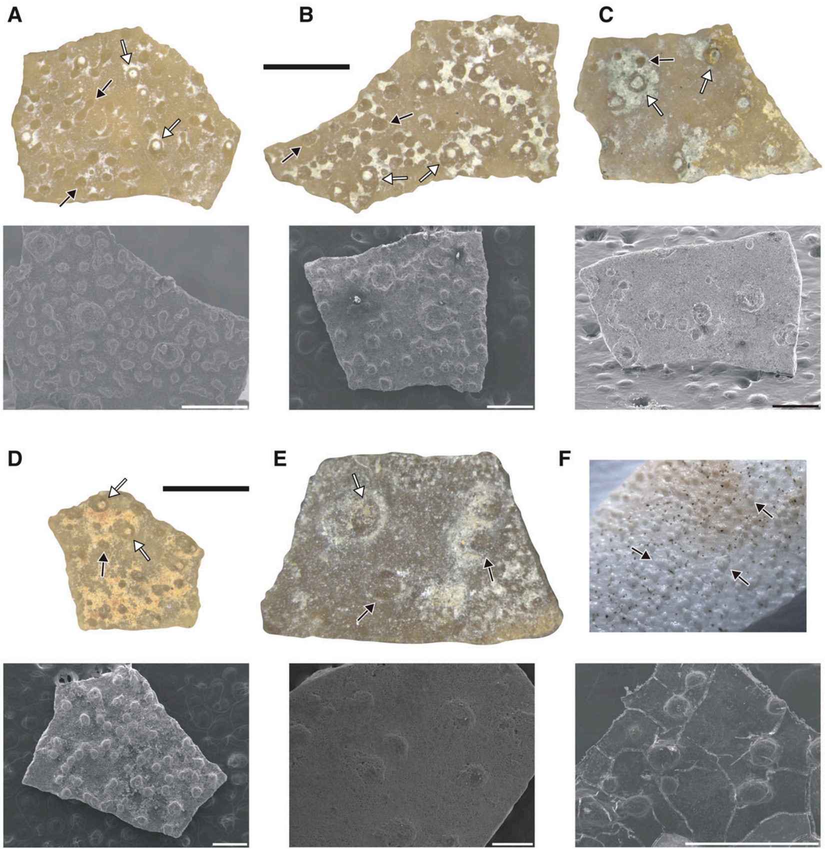


**FIG. 3.** European Late Cretaceous *Pseudogeckoolithus* specimens and extant gecko eggshell, on stereomicroscopy (upper row) and scanning electron microscopy (SEM; lower row), respectively. A, MTM VER 2015. 336a–b, Iharkút. B, LPB [FGGUB] R.2668.3–4, Petrești-Black Lens. C, LPB [FGGUB] R.2669.6–7, Vălioara-Fântânele. D, LPB [FGGUB] R.2672.4–5, Pui-Classic. E, MPZ 2019/573, Blasi 2. F, External view of *Gekko gecko* (Gekkota) eggshell. The dispersituberculate ornamentation and the presence of crater-like (*sensu* Prondvai *et al.* 2017) aspect of the nodes are marked by black and white arrows, respectively. Note the absence of crater-like ornamentation in *Gekko gecko* eggshell. Scale bars represent 1 mm (stereomicroscopy images); 500 μm (SEM images). Colour online.

### *Extant comparative materials*

Modern gekkotan and avian eggshells were analysed in more details, as control groups to provide comparative neontological crystallographic data for the two clades suggested to include the potential egg layers (i.e. Gekkota and Theropoda) of *Pseudogeckoolithus* (see above). Among Gekkota, *Gekko gecko* and *Phelsuma grandis* are members of the Gekkonidae (Gamble *et al.* 2011; Pyron *et al.* 2013) that lay rigid-shelled eggs, and their eggshells show the typical gekkotan crystallographic arrangement (Choi *et al.* 2018). Of these, the *Gekko gecko* eggshell has a nodular ornamentation similar to the dispersituberculate one of *Pseudogeckoolithus* (Fig. 3F), which led to the gekkotan-affinity interpretation of *Pseudogeckoolithus* in the past (e.g. Garcia 2000). The gekkotan eggshell materials included in the present study are those analysed in Choi *et al.* (2018).

We also included in our comparison the eggshells from an emu (*Dromaius novaehollandiae*) and from a domestic duck (*Anas platyrhynchos domesticus*), representing a palaeognath and a neognath bird, respectively. The emu eggshell is particularly appropriate for the purpose of this study because it presents ornamentation on its outer surface (Mikhailov 1997*b*; Grellet-Tinner 2006), which is a very uncommon trait in modern avian eggshells (Hauber 2014). It was found that palaeognath and neognath eggshells have different crystallographic features especially in their misorientation distribution (angular difference between the grains) and *c*-axis alignment (Choi *et al.* 2019*a*), and thus the emu and duck eggshells together cover a representative range of modern avian eggshell diversity. For further information, see Choi *et al.* (2019*a*). The avian eggshells used in this study were both available commercially.

Last, a crocodylian (*Caiman latirostris*) eggshell was also analysed to record the crystallography of the ornamentation in non-dinosaurian archosaur eggshell as well, and to compare it with that of *Pseudogeckoolithus*. The material was provided by Dr Kohei Tanaka (University of Tsukuba) to SC.

### *Electron backscatter diffraction*

We followed the established methods of EBSD analysis of fossil and modern eggshells and data curation (Moreno-Azanza *et al.* 2013, 2017; Choi *et al.* 2018, 2019*a*). The results are presented in inverse pole figure (IPF) maps, lower hemisphere pole figures, grain boundary maps, misorientation histograms, and *d*-value bar charts. Detailed description of the methodology and data curation can be found in Choi *et al.* (2019*b*, text S3).

## RESULTS

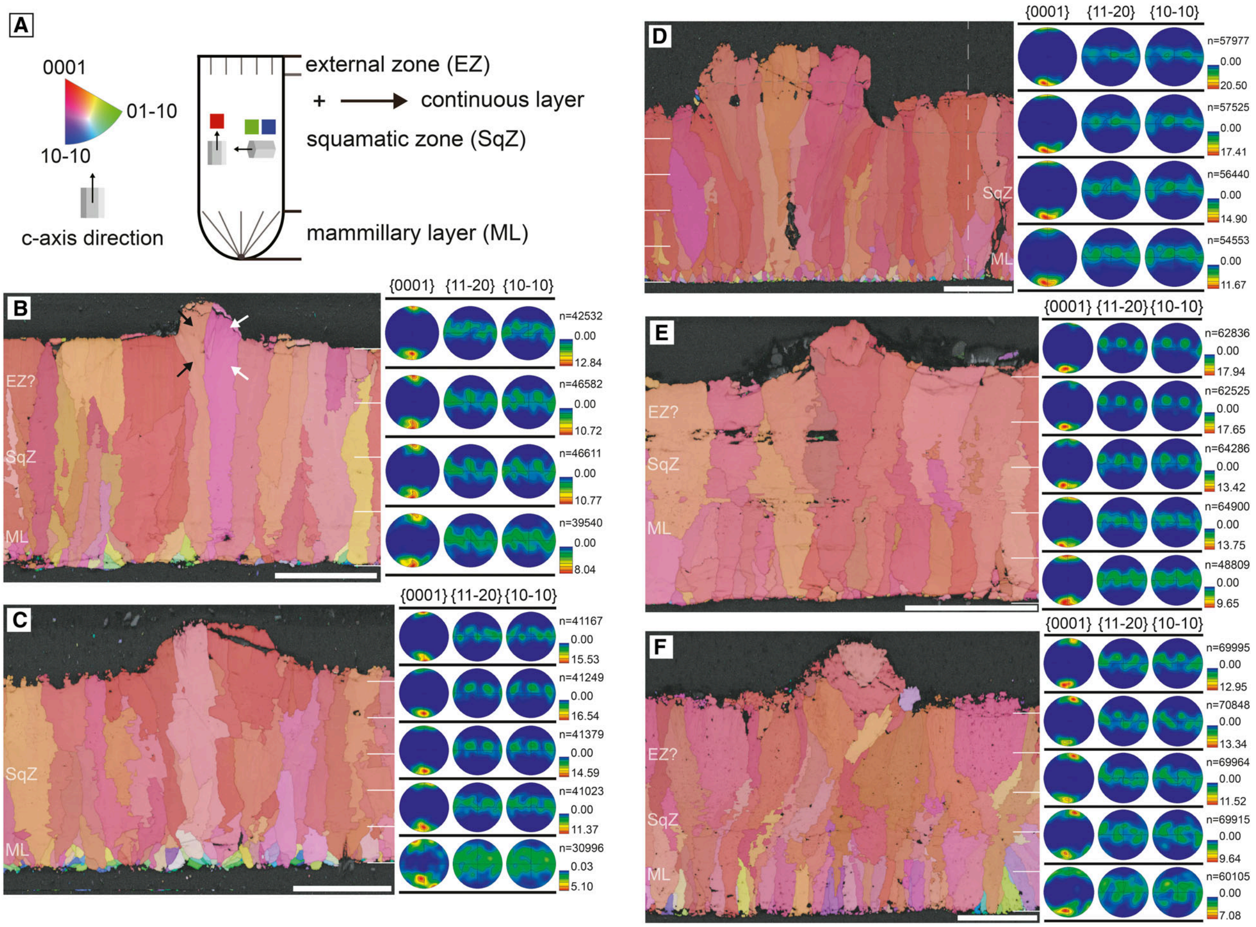
### Crystallography of *Pseudogeckoolithus*

All European *Pseudogeckoolithus* eggshells analysed in the present study share several crystallographic features. First, the *c*-axis alignment generally increases from the inner towards the outer part of the shell (Fig. 4), a typical feature of the archosaurian eggshells (Dalbeck & Cusack 2006; Moreno-Azanza *et al.* 2013, 2017; Choi *et al.* 2019*a*). The shared presence of this pattern in the current sample is also confirmed on multiple of uniform density (MUD) values (see Casella *et al.* 2018 for explanation) 12 along with the lower hemisphere pole figures (Fig. 4). Second, in all sampled *Pseudogeckoolithus* shells the nodular ornamentation shows crystallographic architectural continuity with the underlying continuous layer of the eggshell. The large prismatic crystalline domains that form the continuous layer extend into the ornamentation, with two to three domains that contribute to each tubercle (Fig. 4B), implying that the nodular ornamentation was formed by extended eggshell deposition. Third, all European *Pseudogeckoolithus* shells are characterized by high-angled grain boundaries (>20°) (Fig. 5; Choi *et al.* 2019*a*). The misorientation angular distributions are plotted using histograms with neighbour-pair and random-pair methods (Fig. 5; Choi *et al.* 2019*b*, text S3), and are over 20° on average with the neighbour-pair method. Detailed description and additional EBSD images of *Pseudogeckoolithus* from each locality are provided in Choi *et al.* (2019*b*, text S4 and fig. S1).

### *Comparisons with fossil eggshells*

Both hadrosaur and sauropod eggshells are composed of a single layer in which the crystals comprising the eggshell are homogenous throughout its thickness (Grellet-Tinner *et al.* 2006; Barta *et al.* 2014; Choi *et al.* 2019*b*, fig. S2C–F). In eggshells of both clades, low-angle grain boundaries 16 are widespread (Moreno-Azanza *et al.* 2013, 2016, 2017; Choi *et al.* 2019*b*, fig. S2D, F), and most grain boundaries are linear (Grellet-Tinner *et al.* 2011; Moreno-Azanza *et al.* 2013, 2017; Eagle *et al.* 2015). In all of these features, both sauropod and hadrosaur eggshells are markedly different from those of *Pseudogeckoolithus*.

In contrast, marked microstructural similarities with *Pseudogeckoolithus* are definitively present in both the troodontid and the enantiornithine eggshells (see Choi *et al.* 2019*b*, fig. S2G–J). All of these ootaxa share (1) the existence of an inner mammillary layer and an outer continuous layer, a typical feature of theropod eggshells (Mikhailov 1997*a*); and (2) rugged grain boundaries in



[13] **FIG. 4.** Inverse pole figure (IPF) maps and lower hemisphere pole figures of European *Pseudogeckoolithus*. A, an interpretation key for IPF maps and abbreviations of eggshell layers. See Choi *et al.* (2019*b*, text S3) for details. B, Iharkút (MTM VER 2015. 336c). C, Petreşti-Black Lens (LPB [FGGUB] R.2668.2). D, Vălioara-Fântânele (LPB [FGGUB] R.2669.5). E, Pui-Classic (LPB [FGGUB] R.2672.3). F, Blasi 2 (MPZ 2019/580). D, the outer surface of *Pseudogeckoolithus* (marked by a grey dashed line) is heavily covered with diagenetic calcite overgrowth, which does not reflect genuine biological signal (Choi *et al.* 2019*b*, fig. S3A; see also Choi *et al.* 2019*a*; Kim *et al.* 2019). The lower hemisphere pole figures for this specimen were constructed using the grains lying left to the white dashed line in order not to include a crack. In all specimens, the ornamentation is formed through extended shell deposition (black and white arrows in B). Note that in all cases where the ML is preserved, its inner tip is characterized by calcite grains with a horizontally laid *c*-axis, whereas the *c*-axis alignment becomes generally stronger towards the outer eggshell surface, shown by multiple of uniform density [14] (MUD) values on the lower right of the lower hemisphere pole figures (see also Moreno-Azanza *et al.* 2013, 2017). A MUD of 1 indi- [15] cates randomly oriented grains; a MUD significantly >1 is indicative of a fabric. Scale bars represent 100 μm.

the squamatic zone, which was suggested to be a diagnostic feature (squamatic ultrastructure) in maniraptoran eggshells (Choi *et al.* 2019*a*; see below). Also, the troodontid eggshell and at least some *Pseudogeckoolithus* specimens share the possible existence of an external zone, which may be diagnosed by the presence of linear grain boundaries, in contrast with the rugged grain boundaries present in the squamatic zone lying below (Choi *et al.* 2019*a*; see below). As far as we are aware, there is no known non-theropod dinosaur eggshell that has the aforementioned morphological traits.

### *Comparison with modern eggshell*

*Gekkotan eggs.* The crystallographic architecture of modern gekkotan eggshell is unique among amniotes (Choi *et al.* 2018). The outer quarter of the eggshell is characterized by randomly oriented small calcite grains. The upright *c*-axis alignment (expressed by the intensity of red colour in the IPF map) becomes stronger towards the inner eggshell surface. In addition, the concentration of phosphorus, which is known to function as an inhibitor [17] (as phosphate) of calcite growth (Bachra *et al.* 1963; Lin [18]

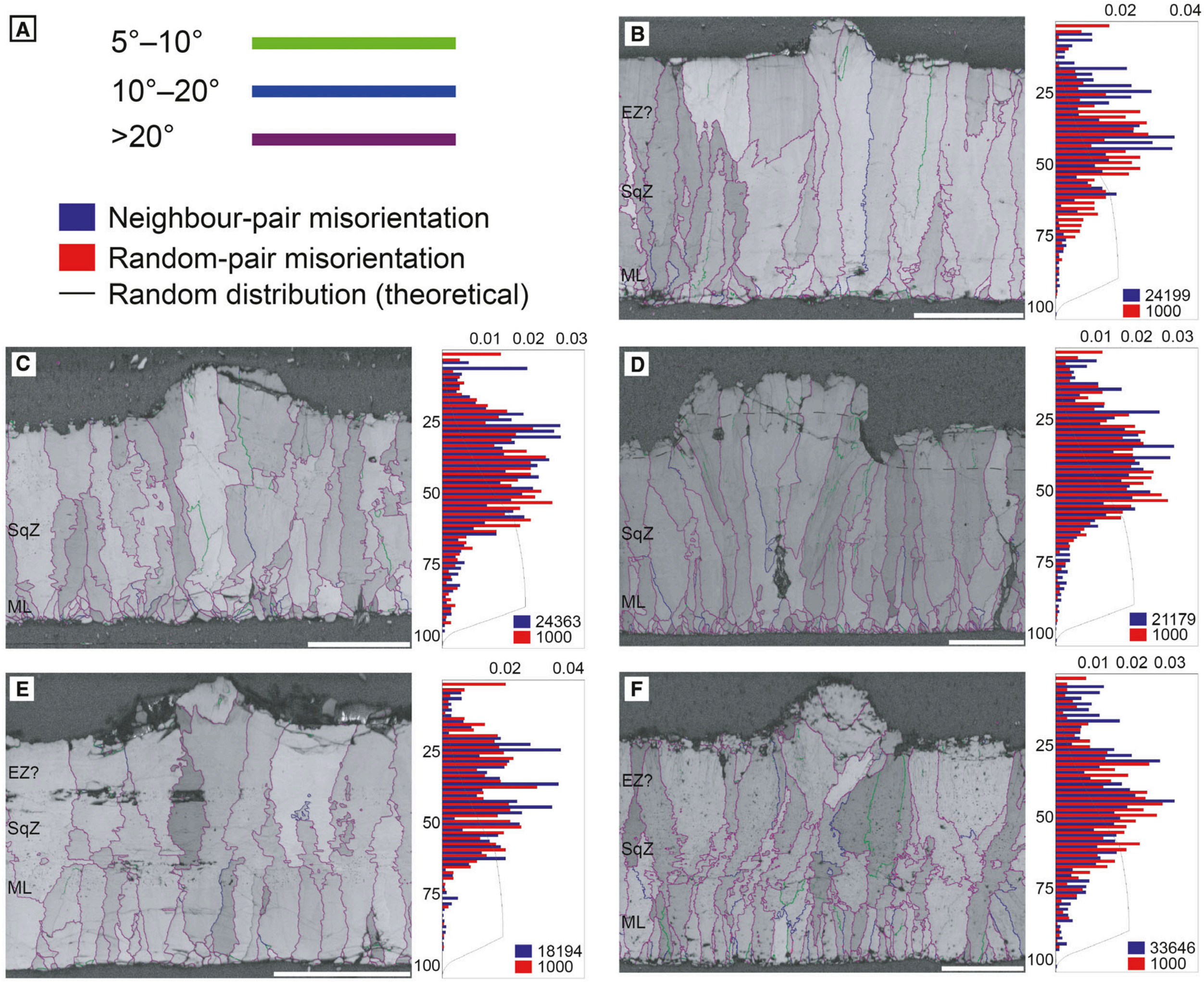


**FIG. 5.** Grain boundary maps and misorientation histograms of European *Pseudogeckoolithus*. A, interpretation keys. See Choi *et al.* (2019*b*) for details. B, Iharkút (MTM VER 2015. 336c). C, Petreşti-Black Lens (LPB [FGGUB] R.2668.2). D, Vălioara-Fântânele (LPB [FGGUB] R.2669.5). E, Pui-Classic (LPB [FGGUB] R.2672.3). F, Blasi 2 (MPZ 2019/580). In all cases, the high-angle grain boundary (>20°; purple line) outnumbers low-angle grain boundary (<20°; blue and green lines). Note rugged grain boundaries in squamatic zone (SqZ) and linear grain boundaries in possible external zone (EZ?), respectively (see Choi *et al.* 2019*b*, fig. S4; Choi *et al.* 2019*a*). The numbers on the vertical and horizontal axes in the histogram mean degree and frequency of misorientation, respectively. *Abbreviation*: ML, mammillary layer. Scale bars represent 100 μm.

& Singer 2005; Chien *et al.* 2008), increases towards the inner surface of the eggshell (Choi *et al.* 2018, figs 7, 8). To the best of our knowledge, these crystallographic and compositional arrangements are observed only in the rigid gekkotan eggshells among amniotes.

The clear-cut crystallographic differences between gekkotan eggshell and *Pseudogeckoolithus* are also strongly expressed in their dispersituberculate ornamentation. Eggshell ornamentation in *Gekko gecko* is made up of randomly aligned calcite grains (Fig. 6A), usually with an enigmatic bulbous structure present inside (fig. S9 in Choi *et al.* 2018). This bulbous structure, however, may not have a crystalline structure given that no Kikuchi pattern (a diffraction pattern used for interpreting the orientation of crystalline material in EBSD analysis) was detected (Fig. 6A; Choi *et al.* 2018). In contrast, the ornamentation in *Pseudogeckoolithus* is made up of compact calcite that is crystallographically continuous with the underlying eggshell units (Fig. 4), and does not contain randomly arranged calcite grains. It also lacks the internal bulbous structure seen in eggshell of *Gekko gecko*.

*Avian eggs.* In all crystallographic aspects, *Pseudogeckoolithus* is very similar to theropod (including avian)

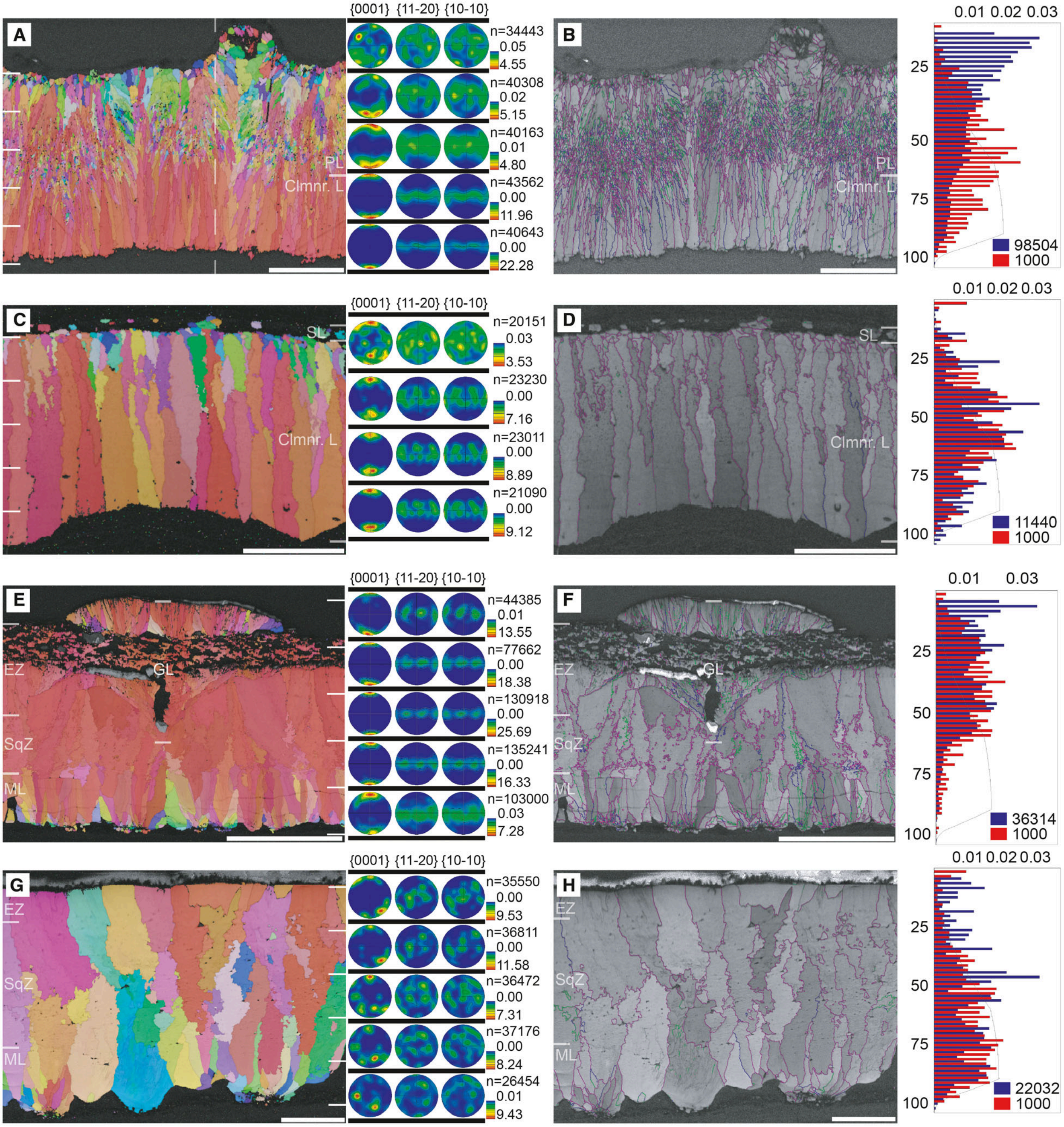


**FIG. 6.** Eggshell electron backscatter diffraction (EBSD) images from modern representatives of the clades hypothesized to include *Pseudogeckoolithus* egg layers. A–B, *Gekko gecko* (Gekkota). C–D, *Phelsuma grandis* (Gekkota). Gekkotan eggshell terminology follows Choi *et al.* (2018). E–F, *Dromaius novaehollandiae* (Aves: Palaeognathae). G–H, *Anas platyrhynchos domesticus* (Aves: Neognathae). In A, the lower hemisphere pole figures were constructed using the grains lying on the left of the white dashed line so that grains potentially influenced by the ornamentation are not included. In gekkotan eggshells (A, C), *c*-axis alignment becomes higher with vertical orientation towards the inner eggshell surface, the opposite pattern to that seen in *Pseudogeckoolithus* (Fig. 4) and extant avian eggshells (E, G; Choi *et al.* 2019*a*). The ornamentation in *Gekko gecko* eggshell is composed of randomly oriented calcite grains; that of emu eggshell is composed of wedge-shaped granular layer (GL) initiated in the middle of the squamatic zone (SqZ). Both of them are crystallographically discontinuous with the underlying eggshell. Note the trilaminate structure observed due to grain ruggedness in avian eggshell (F, H), similar to that seen in the Pui-Classic and Blasi 2 *Pseudogeckoolithus* (Fig. 4E, F). *Gekko gecko* eggshell has a low-angle-dominant misorientation distribution (B) compared with that of *Phelsuma grandis* eggshell (D). Key to EBSD interpretation as in Figures 4A, 5A. *Abbreviations:* Clmnr. L, columnar layer; EZ, external zone; ML, mammillary layer; PL, XXX; SL, XXX. Scale bars represent 100 μm (A, B, G, H); 50 μm (C, D); 500 μm (E, F).

eggshell (Fig. 6E–H; Choi *et al.* 2019*b*, fig. S2G–J; see Choi *et al.* 2019*a* for EBSD analysis of further fossil and extant maniraptoran eggshells). In theropod eggshells, the calcite grains begin to radiate from the eisospherite in the mammillary layer (Fig. 6E–H). When they join inside the continuous layer, calcite grains are usually aligned with their *c*-axis lying perpendicular to the eggshell surface (Fig. 6E, G; see also Dalbeck & Cusack 2006; Moreno-Azanza *et al.* 2013; Choi *et al.* 2019*a*).

In the *Dromaius* (emu) eggshell there is a granular layer (GL; *sensu* Mikhailov 1997*b*) initiated in the middle of the squamatic zone (Fig. 6E) that forms a peculiar, hillock-like ornamentation (*sensu* Grellet-Tinner 2006). This ornamentation is, however, crystallographically discontinuous with the main eggshell microstructure, thus different from the ornamentation of *Pseudogeckoolithus* (Fig. 4). The *Anas* (domestic duck) eggshell is smooth and unornamented, as is the case for almost all modern avian egg- 21 shells.

Except for the presence of a nodular dispersituberculate ornamentation, the crystallographic arrangement of the European *Pseudogeckoolithus* is especially similar to that of the typical palaeognath eggshell as well as to that of *Gobioolithus minor*, an enantiornithine ootaxon (Mikhailov 1996; Kurochkin *et al.* 2013), in that the upright *c*-axis alignment is stronger than that present in neognath eggshells (Fig. 6G; Choi *et al.* 2019*a*). More interestingly, *Pseudogeckoolithus* specimens from two fossil localities surveyed here, Pui-Classic in Romania and Blasi 2 in Spain (Fig. 5E, F) show a marked difference in microstructure compared with the other *Pseudogeckoolithus* materials studied (Fig. 5B–D), but are similar to the troodontid eggshell (*Prismatoolithus levis*), in that rugged grain boundaries in the squamatic zone change into linear grain boundaries in the external part of the eggshells; this feature is very clearly seen in the emu eggshell, and is also present in the duck eggshell (Fig. 6E–H). The presence of an overlying zone with linear grain boundaries has been postulated as a valid criterion for identifying the external zone (Choi *et al.* 2019*a*, *b*, fig. S4), a well-known trait of modern avian eggshell (Mikhailov 1997*b*). Although the existence of an external zone must be confirmed by detailed ultrastructural study using scanning electron micrcoscopy, the occurrence of a linear grain boundary near the outer shell surface suggests that an external zone may be also present at least in some *Pseudogeckoolithus*.

Finally, in several types of avian eggshells examined – namely in *Gallus* (chicken; Cusack *et al.* 2003), *Struthio* (ostrich) and *Dromaius* (Dauphin *et al.* 2006; Choi *et al.* 2019*b*, fig. S3B) as well as *Pica* (Eurasian magpie; Choi *et al.* 2019*b*, fig. S3C) eggshells – the concentration of phosphorus increases towards the outer surface, in contrast to the pattern present in gekkotan eggshell. To conclude, the crystallography and chemical composition of the gekkotan eggshells suggest an opposing growth direction compared with that seen in archosaurian eggshells, and is similarly opposite to that present in *Pseudogeckoolithus* (Fig. 6A, C; Choi *et al.* 2018).

*Crocodylian eggs.* Crocodylian eggshell is also characterized by the presence of ornamentation (Schleich & Kästle 1988), but there is no nodular ornamentation in such an eggshell; instead, most of it is pointed (e.g. Choi *et al.* 2019*b*, fig. S2A, B) or even more complicated in shape (e.g. Schleich & Kästle 1988; Cedillo-Leal *et al.* 2017). The crystals forming crocodylian eggshell are usually wedge shaped (Mikhailov 1997*a*; Choi *et al.* 2019*b*, fig. S2A), thus, it can be easily differentiated from maniraptoran eggshell. Accordingly, the possibility of a crocodylian affinity for *Pseudogeckoolithus* is minimal.

### d-*value of diverse sauropsid eggshells*

We applied the Kolmogorov–Smirnov test to check for quantitative differences between the neighbour- and random-pair misorientation distributions of *Pseudogeckoolithus* using *d*-value (Figs 5, 7; Choi *et al.* 2019*a*). The higher the *d*-value, the more likely it is that ‘neighbouring lattices know about each other in a way that distant (=randomly chosen) lattices do not’ (see Wheeler *et al.* 22 2001, p. 113 for details). In addition, to cover the wider range of *d*-values in sauropsid eggshell, we expanded the dataset in Choi *et al.* (2019*a*, *b*), fig. S4), which consisted only of maniraptoran eggshells.

Except for one Vălioara-Fântânele specimen, all *Pseudogeckoolithus* have a *d*-value higher than 1.949, meaning that the neighbour- and the random-paired misorientations have a statistically significantly different distribution 25 with probability higher than 0.999 (Fig. 7). The Vălioara-Fântânele material has a *d*-value of 1.36, but its neighbour- and random-paired misorientations are still different with a probability higher than 0.95. The resulting *d*-values were consistent in all European *Pseudogeckoolithus* specimens investigated with the type 2 distribution typical of maniraptoran eggshells, as documented by Choi *et al.* (2019*a*).

We also calculated *d*-values for additional non-*Pseudogeckoolithus* eggshells analysed in this study as well as those presented elsewhere alongside EBSD data (Moreno-Azanza *et al.* 2013, 2016, 2017; Choi & Lee 2019). These sample eggshells can be grouped into three categories: (1) maniraptoran eggshells (*Dromaius*, *Reticuloolithus acicularis* and *Trigonoolithus amoae*); (2) non-maniraptoran archosaur eggshells (*Caiman latirostris*, cf. *Maiasaura*, *Guegoolithus turolensis* and *Megaloolithus* cf. *siruguei*); and (3) gekkotan eggshells (*Gekko gecko* and *Phelsuma*

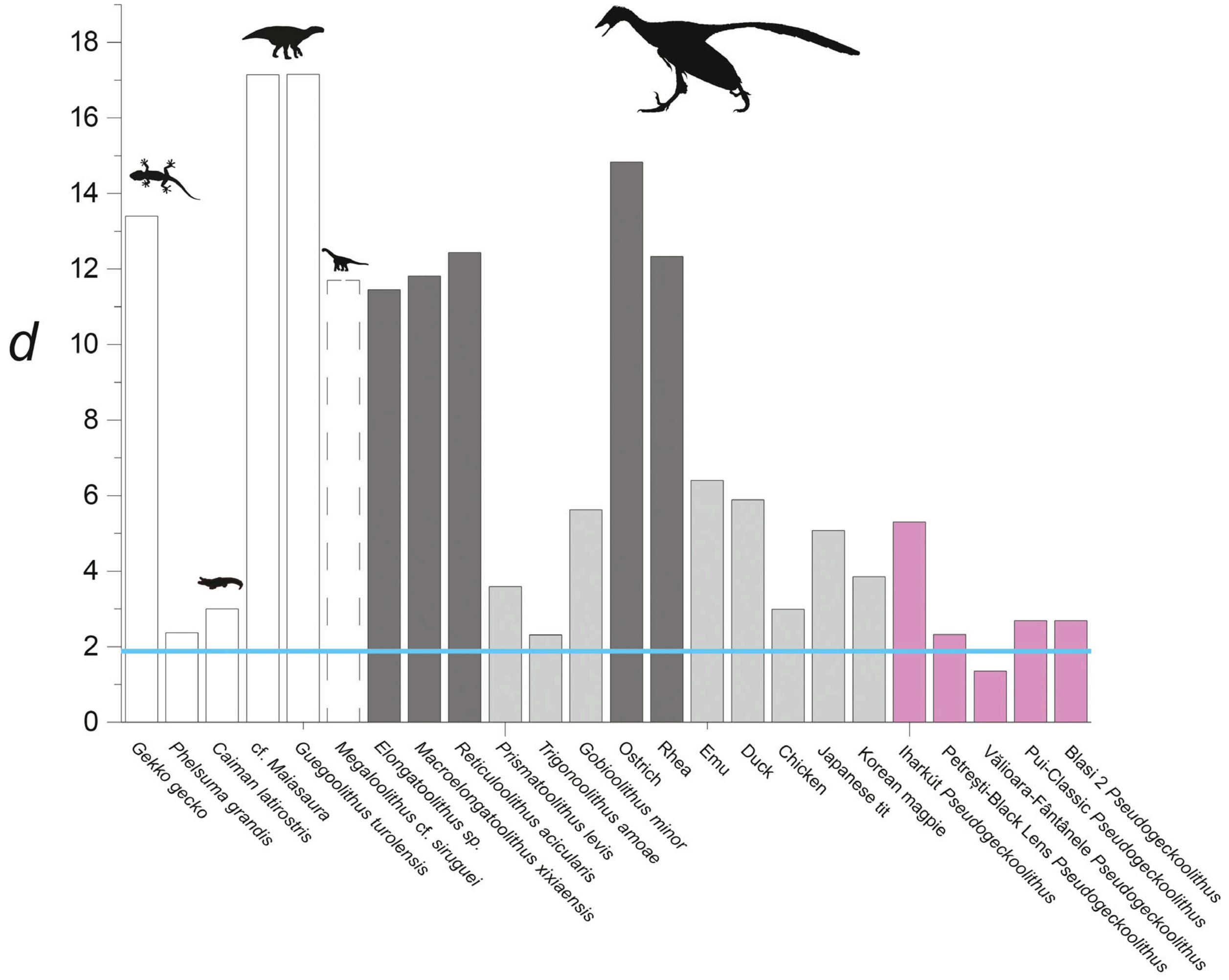


**FIG. 7.** *d*-value of diverse sauropsid eggshells. Maniraptoran eggshells are coloured and are subdivided into *Pseudogeckoolithus* (pink), type 1 distribution eggshells (dark grey) and type 2 distribution eggshells (light grey). The sauropod eggshell bar marked by dashed lines was based on taphonomically influenced material (Moreno-Azanza *et al.* 2016). A blue line marks the *d*-value of 1.949, above which the neighbour- and the random-paired misorientations have a statistically significantly different distribution with probability higher than 0.999. The source of *d*-values not originally calculated in this study are: Choi *et al.* (2019*a*); Choi & Lee (2019). Silhouettes: *Archaeopteryx*, Scott Hartman (http://www.phylopic.org); *Gekko*, *Caiman*, hadrosaur and sauropod, SC.

*grandis*). *Trigonoolithus* showed typical type 2 distribution as anticipated in Choi *et al.* (2019*a*). In the case of the *Dromaius* eggshells, the *d*-value was more similar to the type 2 distribution, although it has the highest *d*-values compared with other type 2 eggshells and still has a significant amount of low-angle grain boundaries under the neighbour-pair method (Fig. 6F), similar to the ostrich and rhea eggshells (Choi *et al.* 2019*a*). The ostrich and rhea eggshells used in Choi *et al.* (2019*a*) had much higher *d*-values (>12), and thus the case of *Dromaius* shows that not all palaeognath eggshells have a clear type 1 distribution; instead, some of these demonstrate a transitional state when it comes to misorientation distribution. In contrast, ornithischian eggshells (cf. *Maiasaura* and *Guegoolithus*) have the highest *d*-values (>17). The sauropod eggshell (*Megaloolithus* cf. *siruguei*) also has a higher *d*-value, but we would like to consider this as a provisional result because it is based on a taphonomically altered sauropod eggshell (Moreno-Azanza *et al.* 2016) and should be updated with the results derived from better preserved material (e.g. Grellet-Tinner *et al.* 2011). The *Caiman latirostris* eggshell has a lower *d*-value, similar to the type 2 distribution of maniraptoran eggshells. Finally, the two gekkotan eggshells show a remarkable contrast in their *d*-values. The *d*-value of the *Gekko gecko* eggshell was similar to the type 1 distribution of maniraptoran eggshell, while *Phelsuma grandis* presents the type 2 distribution of maniraptoran eggshell.

# DISCUSSION

## Maniraptoran affinity of *Pseudogeckoolithus*

The crystallographic features identified on EBSD analysis clearly show that *Pseudogeckoolithus* is definitively not a squamate eggshell. Crystallographic contrasts documented both in overall eggshell microstructure per se and in ornamentation between the *Gekko gecko* eggshell and *Pseudogeckoolithus* document the action of markedly different building pathways that underlay their distinctive architectures. Their apparently highly similar nodular ornamentations are thus truly homoplastic, and, more specifically, convergent *sensu* Hall (2003; i.e. they represent similarities arising through independent evolution via different developmental pathways). Accordingly, in line with the original interpretation of Vianey-Liaud & Lopez-Martinez (1997) and, more recently, of Prondvai *et al.* (2017), but *contra* Garcia (2000) and Sellés (2012), we firmly establish here the non-gekkotan affinity of the *Pseudogeckoolithus* material surveyed in this study. Furthermore, we suggest that the previously proposed gekkotan origin of other Late Cretaceous European ‘geckoid’ eggshell materials, such as that of morphotype geckonoïde of Garcia (2000), should undergo similar scrutiny, given that it shows remarkable external and microstructural similarity to the *Pseudogeckoolithus* materials studied herein.

Based on the aforementioned features and comparisons, *Pseudogeckoolithus* can be safely identified as a theropod eggshell. Indeed, *Pseudogeckoolithus* has at least a two-layered structure made up of a mammillary layer and a squamatic zone (Fig. 4A). This bilaminate structure is absent in sauropod (Grellet-Tinner *et al.* 2006; Moreno-Azanza *et al.* 2016) and ornithischian (Barta *et al.* 2014; Moreno-Azanza *et al.* 2017) eggshells, which are composed of a single layer (mammillae extending up to the outer eggshell surface; see also supplementary text in Stein *et al.* 2019), whereas it is ubiquitous in known extinct and modern maniraptoran eggshells (Mikhailov 1997*a*, *b*; Choi *et al.* 2019*a*). Also, hadrosaur and sauropod eggshells have abundant low-angle grain boundaries, whereas such are rarely observed in *Pseudogeckoolithus*. All these observations eliminate any potential hadrosaur or sauropod affinity for *Pseudogeckoolithus*, not to mention the extreme thinness of *Pseudogeckoolithus*, compared with the eggshells typical for the other two clades.

In contrast, admittedly, non-maniraptoran theropod eggs are as yet poorly known: the only definite cases are represented by eggs ascribed to the megalosaurid *Torvosaurus* (Carrano *et al.* 2012) and to the allosauroid *Lourinhanosaurus* (Malafaia *et al.* 2017), both from the Upper Jurassic of Portugal (Araújo *et al.* 2013; Ribeiro *et al.* 2014). The eggshell of *Torvosaurus* has only a single layer (Araújo *et al.* 2013; Ribeiro *et al.* 2014), whereas that of *Lourinhanosaurus* is two-layered (Mateus *et al.* 1997; Ribeiro *et al.* 2014), similar to the typical maniraptoran eggshell. However, whether the two-layered structure of the *Lourinhanosaurus* eggshell has a similar crystallographic make-up to those of the maniraptorans is as yet unknown, and should be clarified (Choi & Lee 2019).

To conclude, within Theropoda, *Pseudogeckoolithus* can be assigned to a maniraptoran egg-layer on the basis of (1) a two-layered structure, with the presence of a mammillary layer and a continuous layer, character shared with all maniraptoran taxa (Mikhailov 1997*a*) and with the allosauroid *Lourinhanosaurus* (Mateus *et al.* 1997; Ribeiro *et al.* 2014); (2) an angusticanaliculate pore system (Prondvai *et al.* 2017), shared with most maniraptorans including Aves (Mikhailov 1997*a*); and (3) the possible existence of an external zone, a character widespread within avian eggshells (Mikhailov 1997*b*) and which is also present in some derived maniraptorans eggshells (e.g. *Trigonoolithus amoae*, *Triprismatoolithus stephensi* and *Prismatoolithus levis*; Varricchio & Jackson 2004, 2010; Jackson & Varricchio 2010; Moreno-Azanza 26 *et al.* 2014*b*). Moreover, its greatly reduced thickness, suggestive of [a] small-sized theropod egg-layer[s] (Prondvai *et al.* 2017), may further support its maniraptoran affinity, given that most Late Cretaceous European maniraptorans (including non-avian paravians; the theropods of unknown affinity *Richardoestesia* and *Euronychodon*; as well as enantiornithine and ornithurine birds; Csiki-Sava *et al.* 2015) are characterized by small body size. Meanwhile, it is worth noting that all known non-maniraptoran Late Cretaceous theropods from Europe (abelisauroids, basal tetanurans) were medium- to large-sized animals (Csiki-Sava *et al.* 2015). Such a mutually exclusive body size distribution among the Late Cretaceous theropods of Europe minimizes the possibility that *Pseudogeckoolithus* is an ootaxon of a medium- to large-sized non-maniraptoran theropod, considering the known positive correlations between adult body mass and egg size in extant Aves (Juang *et al.* 2017), and that between egg mass (hence, size) and eggshell thickness (Ar *et al.* 27 1979).

Nevertheless, further specimens, including more complete eggs (or fortuitous discoveries such as *in ovo* embryos or gravid females), are needed to firmly establish the affinity of *Pseudogeckoolithus*, given that assigning a particular ootaxon to a certain clade can be erroneous in the absence of an embryo preserved *in ovo* (see discussion in Choi & Lee 2019). Embryo *in ovo* specimens would also narrow the assignment of the *Pseudogeckoolithus* eggs to one of the maniraptoran groups that were present in

Europe at the end of the Cretaceous. It is worth noting, nonetheless, that eggs and eggshells from the Maastrichtian of Romania reported to co-occur with skeletal remains of (and thus referred to) taxonomically indeterminate enantiornithines (Dyke *et al.* 2012) differ markedly in their ornamentation pattern (Fernández *et al.* 2019) from the typical dispersituberculate ornamentation of *Pseudogeckoolithus*.

### *EBSD, an adequate tool to identify true fossil gekkotan eggshell*

Our EBSD analyses clearly show that *Pseudogeckoolithus* is not a gekkotan-related ootaxon; instead, it can be safely identified as belonging to a maniraptoran theropod group. In future studies, our approach can be extended and it should be applied to other putative fossil squamate eggshells (Choi *et al.* 2019*b*, table S1; text S5) in order to rigorously determine their accurate crystallographic arrangement and thereby assess the most likely phylogenetic affinity. Equally importantly, there are further documented examples of rigid squamate eggshell producers, both extant and fossil, such as the diplodactylid gekkotan *Eurydactylodes* (it may have acquired a rigid eggshell independently from other gekkotan families; Kratochvil & Frynta 2006), some Dibamidae (Choi *et al.* 2018), and certain fossil Anguimorpha (Fernandez *et al.* 2015). It is not yet known whether the peculiar and very characteristic crystallographic arrangement of the rigid gecko eggshell (Choi *et al.* 2018) is autapomorphic, or whether it is more widespread among the rigid eggshell-producing squamates. Therefore, fossil rigid eggshells that are found without an associated embryo *in ovo*, and are probably not of archosauromorph origin, currently can be identified neither as gekkotan, nor as non-gekkotan squamate eggshells with certainty. Hence, for a comprehensive understanding of rigid eggshell evolution in Squamata, and in amniotes in general, as well as for correct taxonomic identification of fossil squamate eggshells, additional modern and fossil samples should also be analysed using EBSD.

### Eggshell ornamentation in extant megapode birds, *Gekko gecko* and fossil maniraptorans

In extant sauropsids, gekkotan and crocodylian eggshells regularly exhibit ornamentation (Schleich & Kästle 1988; Marzola *et al.* 2015; Cedillo-Leal *et al.* 2017; Choi *et al.* 2018), while this is mostly absent in avian eggshells. Rare exceptions to the latter pattern are the nodular eggshell ornamentation of megapodes (Galliformes, Neognathae; Grellet-Tinner *et al.* 2017) and the modest hillock-like ornamentation found in cassowary and emu (Casuariidae, Palaeognathae; Mikhailov 1997*b*; Zelenitsky & Modesto 2003; Grellet-Tinner 2006; Lawver & Boyd 2018). Although many Cretaceous and Palaeogene avian eggshells also lacked ornamentation (Mikhailov 1996; Grellet-Tinner & Dyke 2005; Jackson *et al.* 2013; Varricchio & Barta 2015; Fernández *et al.* 2019), this condition was probably not always the dominant phenotype throughout avian evolutionary history. For example, the Palaeogene *Metoolithus nebraskensis* (Jackson *et al.* 2013) and *M. jacksonae* (Lawver & Boyd 2018), as well as *Ornitholithus* (Donaire & López-Martínez 2009; Angst *et al.* 2015) are all recognized as ornamented avian eggshells. Furthermore, ornamentation characterizes the eggshells of diverse Cretaceous non-avian maniraptorans (e.g. *Deinonychus* eggshell, Elongatoolithidae, *Nipponoolithus*, *Reticuloolithus*, *Trigonoolithus* and *Triprismatoolithus*; Mikhailov 1997*a*; Grellet-Tinner & Makovicky 2006; Jackson & Varricchio 2010; Moreno-Azanza *et al.* 2014*b*; Tanaka *et al.* 2016; Choi & Lee 2019), members of the dinosaur clade giving rise to birds. Thus, ornamentation is highly likely to be a plesiomorphic character of the maniraptoran eggshell that disappeared in some extinct and most modern avian taxa (Lawver & Boyd 2018).

The maniraptoran affinity of *Pseudogeckoolithus* verified in the present study raises the question of why extremely similar dispersituberculate ornamentation exists in eggshells of such distantly related clades as Maniraptora and Squamata. Eggshells of extant megapode birds and *Gekko gecko* possess ornamentation with discrete and sparse nodes (Grellet-Tinner *et al.* 2017; Choi *et al.* 2018), and a gecko-like dispersituberculate ornamentation is now also documented in the extinct maniraptoran *Pseudogeckoolithus*. Even though the nodular eggshell ornamentation seen in the modern maniraptoran megapodes is somewhat different in its gross morphology from that of the extinct maniraptoran *Pseudogeckoolithus*, megapode and *Pseudogeckoolithus* eggshells share similar basic crystallographic features. In the megapodes *Alectura lathami* and *Leipoa ocellata* the eggshell ornamentation is formed through extended shell deposition (Grellet-Tinner *et al.* 2017), just as we document here in *Pseudogeckoolithus* (Fig. 4). This type of crystallographic make-up was also reported in oviraptorosaur eggshells (*Elongatoolithus*, *Macroelongatoolithus*; Choi *et al.* 2019*a*), although the ornamentation pattern itself is usually different in its morphology, being linear (Mikhailov 1997*a*) rather than nodular as in *Pseudogeckoolithus* (but also note that *Macroelongatoolithus* possesses dispersituberculate ornamentation as well; Simon *et al.* 2019). In addition, ornamentation of the anguimorph eggshell from the Lower Cretaceous of Thailand (Fernandez *et al.* 2015) also shows morphological similarity with that of the megapode eggshell. It is the only definitive case of squamate eggshell known in the fossil record (identification supported by associated *in ovo* embryos), meaning that rigid eggshell and its nodular ornamentation are not unique traits of gecko eggshells within squamates, but may have been more widespread among their fossil representatives.

The reason for the presence of ornamentation in sauropsid eggshell is a neglected topic in vertebrate palaeontology, except for one speculation (Grellet-Tinner *et al.* 2017). Although the nesting microenvironment of *Gekko gecko* has never been studied, there are several studies on the nesting microenvironment of megapodes. Megapode eggs, which are buried in various substrates and are incubated by environmental heat instead of body heat (Booth & Thompson 1991), have a comparatively thinner shell than eggs laid by similar-sized avian taxa that use body heat in contact incubation. This relative thinness of the megapode eggshell was suggested to represent an adaptation that enhances gas exchange in the peculiar covered nesting environment of megapodes (Booth & Thompson 1991; Harris *et al.* 2014; Grellet-Tinner *et al.* 2017; but see Birchard & Deeming 2009 for an opposing view). Among maniraptoran-related ootaxa, the European *Pseudogeckoolithus* eggshells are also characterized by their remarkable thinness (Table 1; Choi *et al.* 2019*b*, text S4; Prondvai *et al.* 2017).

Given that the megapode and the *G. gecko* eggshell ornamentation represent outlier characters within their own clades (Aves and Gekkota, respectively), their similar gross morphology despite marked differences in underlying crystallographic make-up (resulting from different formational pathways, as shown by EBSD; see Choi *et al.* 2019*b*, text S6 for our view on the eggshell as an end-product of a complex eggshell calcite growth mechanism) may suggest an adaptive significance of this discrete nodular pattern of ornamentation, possibly driven by some kind of similar selection pressure in maniraptorans and gekkotans. Likewise, given that megapodes are derived neornithine maniraptorans (Prum *et al.* 2015), their eggshell ornamentation, which is similar only to that of the distantly related Cretaceous maniraptoran *Pseudogeckoolithus*is, is most likely to be a homoplastic feature that may have been caused by similar nesting microenvironmental settings in megapodes and *Pseudogeckoolithus* (see below). For these reasons, the eggshells of *G. gecko* and/or megapodes might be functionally comparable with, and informative for the interpretation of, the Santonian–Maastrichtian dispersituberculate theropod eggshells, including *Pseudogeckoolithus* (Table 1). Nevertheless, an alternative explanation, namely that this similarity in ornamentation may be only a random outcome of genetic drift and thus represents a non-adaptive retention or novel development of a functionless (and harmless) character in either clade (Gould & Lewontin 1979; Losos 2011), should not be overlooked.

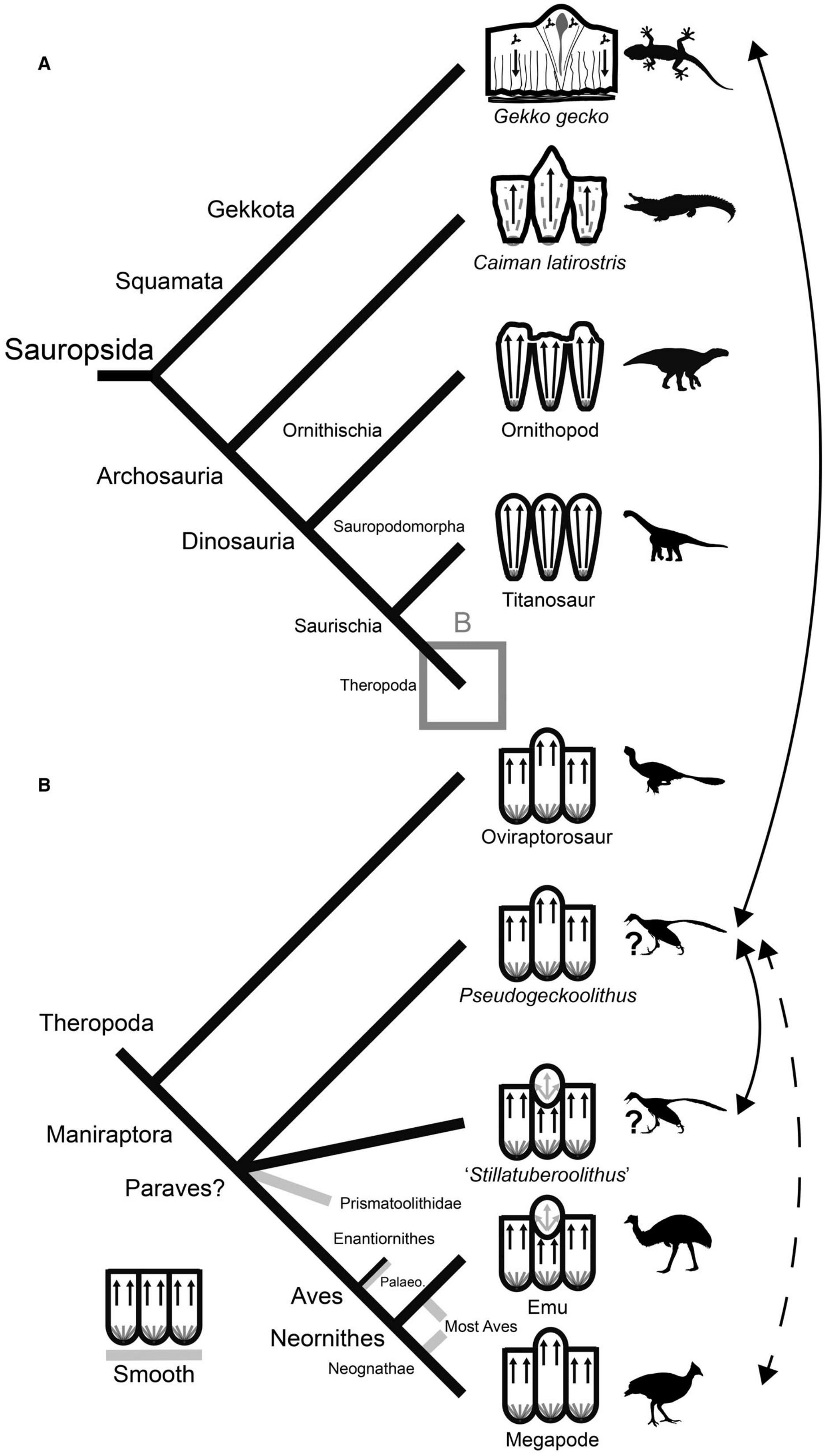
We suggest that neontological experimental data should be gathered by ornithologists and/or herpetologists from the aforementioned extant taxa to shed light on the reason(s), if any, behind the presence of eggshell ornamentation, a feature that represented a dominant phenotypical trend for Mesozoic maniraptoran eggshells (Table 1). Experimental approaches to test its possible role(s), such as those implemented by Cedillo-Leal *et al.* (2017) for crocodylian eggshells, as well as detailed observations on the nesting microenvironments of megapodes and *Gekko gecko*, compared with those of other avian and gekkotan taxa, could help to clarify the evolutionary significance of eggshell ornamentation. This in turn might offer further insights into the reproductive palaeobiology of other dinosaurian and squamate clades with ornamented eggshells (Mikhailov 1997*a*; Fernandez *et al.* 2015), and may also give hints as to why eggshell ornamentation has disappeared in the majority of modern birds (Hauber 2014; Lawver & Boyd 2018).

### *Misorientation pattern in sauropsid eggshells*

The presence of a crystallographic dichotomy (i.e. type 1 and 2 misorientation distributions) within extinct and modern maniraptoran eggshells was first reported in Choi *et al.* (2019*a*). The enlarged dataset used in the present study provides further insights into the crystallographic features of diverse sauropsid eggshells.

First, in Choi *et al.* (2019*a*), palaeognaths were represented only by ostrich and rhea, which both have definitive type 1 distribution. However, the current study documents that the eggshell of the palaeognath *Dromaius* has a more type 2-like distribution (at least in its *d*-value), similar to that of the neognath eggshells (Fig. 7), a finding that is further supported by the rarity of low-angled grain boundary in the emu eggshell (Fig. 6F). This implies that the distribution of type 1 and type 2 crystallographic patterns in avian eggshells is more complicated than that presented in Choi *et al.* (2019*a*, fig. 10), and thus a phylogenetically controlled sample derived from a wide range of avian clades, including palaeognaths and neognaths, should be analysed to better understand the evolutionary pattern.

Second, two ornithopod and sauropod eggshells analysed in this study yielded high *d*-values (we would refrain from using the term 'type 1' distribution for non-maniraptoran eggshells because it was initially coined only for maniraptoran eggshells, and furthermore, the question of whether the high *d*-value seen in ornithopod and sauropod eggshells and the type 1 distribution of maniraptoran eggshells were both inherited from their common ancestor is far from being answered). Although the *d*-value obtained for the sauropod eggshell in the present study


A
Gekko gecko
Gekkota
Caiman latirostris
Squamata
Sauropsida
Ornithopod
Ornithischia
Archosauria
Sauropodomorpha
Dinosauria
Titanosaur
Saurischia
B
Theropoda
B
Oviraptorosaur
?
Pseudogeckoolithus
Theropoda
?
Maniraptora
'Stillatuberoolithus'
Paraves?
Prismatoolithidae
Enantiornithes
Palaeo.
Aves
Emu
Most Aves
Neornithes
Smooth
Neognathae
Megapode

should be double-checked using better preserved eggshells, the results – if upheld –imply that, in general, higher *d*-values (such as those found in the maniraptoran type 1 distribution) may be more widespread within Dinosauria than the lower *d*-values, and that the lower *d*-values may be correlated with the unique reproductive strategy of maniraptoran dinosaurs (i.e. contact incubation; Varricchio & Jackson 2016; Choi *et al.* 2019*a* and references therein). Admittedly, this inference should be further checked using a more comprehensive sample of sauropod and ornithischian dinosaur eggshell material because (as documented in the case of the *Dromaius* eggshell, above) the phylogenetic distribution of high and low *d*-values may be rather complicated and can only be clarified through an extensive investigation. Nevertheless, the present results provide a first glimpse into the *d*-value distribution of non-maniraptoran dinosaur eggshells.

Finally, even though only two gekkotan species were analysed in this respect, surprisingly they show contrasting *d*-values. Similar to the case of maniraptoran eggshells reported by Choi *et al.* (2019*a*), a crystallographic dichotomy may also be present in gekkotan (or squamate, in general) eggshells, reinforcing the need for future comparative investigations into the microstructure and crystallography of a diverse array of squamate eggshells (see above).

### *Detecting homoplasy in eggshell evolution*

Ornamentation morphology has been widely used as a criterion to classify ootaxa at the oofamily level (e.g. Mikhailov *et al.* 1996). However, the present results imply that ornamentation (similarly to other characters such as egg shape, shell unit shape and pore system; Mikhailov 1997*a*) is also prone to homoplasy (Fig. 8).

*Pseudogeckoolithus*, '*Stillatuberoolithus*', *Macroelongatoolithus*, a fossil anguimorph eggshell, as well as eggshell of *Gekko gecko*, megapodes, cassowary and emu, are all characterized by surface ornamentation although the morphology varies (Figs 4–6, 8; Mikhailov 1997*b*; Zelenitsky & Modesto 2003; Grellet-Tinner 2006; Fernandez *et al.* 2015; Grellet-Tinner *et al.* 2017; Oser 2018; Choi *et al.* 2018, 2019*a*). We have shown that the similar-looking dispersituberculate eggshell ornamentation of *Pseudogeckoolithus* and *Gekko gecko* represents a clear case of convergent evolution. Meanwhile, the presence of uniform crystallography of the eggshell ornamentation (formed via extended deposition of the calcite grains) in the more closely related maniraptorans *Pseudogeckoolithus*, oviraptorosaurs (e.g. *Macroelongatoolithus*) and megapodes (Fig. 8; Grellet-Tinner *et al.* 2017; Choi *et al.* 2019*a*) documents the emergence of a common pathway of ornamentation building in maniraptoran eggshells, despite their different overall (or gross) morphology. Such a pathway appears to be a widely used template in ornamentation building in sauropsid eggshells (Fig. 8). In the case of '*Stillatuberoolithus*' and of the extant *Dromaius* eggshells, however, the surface ornamentation is not crystallographically continuous with the underlying eggshell (Fig. 6E, F; Oser 2018). Instead, the appearance of ornamentation is 'programmed' crystallographically in the middle of the squamatic zone (Fig. 8), a feature so distinctive that the ornamentation was actually interpreted as a fourth layer in the case of the *Dromaius* eggshell by Grellet-Tinner (2006).

In summary, there are at least three different ways of producing dispersituberculate ornamentation in sauropsid eggshells: the gecko style; the *Pseudogeckoolithus* style; and the '*Stillatuberoolithus*' style; which can be unambiguously detected on EBSD analysis. The occurrence and distribution of these three different crystallographic patterns of ornamentation building in sauropsid eggshells document clear cases of homoplasy (Fig. 8). Considering that the eggs of almost all modern avian taxa have lost ornamentation (see above), the similarity recorded between *Pseudogeckoolithus* and the megapode eggshell is probably homoplastic unless an alternative scenario is true: that a relict ornamentation of a non-avian maniraptoran eggshell is uniquely retained by an avian clade, the megapodes.

**FIG. 8.** Three types of ornamentation construction pathway in sauropsid eggshells and possible homoplasies. A, schematic crystallography of non-maniraptoran sauropsid eggshells used in this study. B, schematic crystallography of maniraptoran eggshells. In almost all sauropsid eggshells including *Pseudogeckoolithus*, ornamentation is crystallographically continuous with underlying eggshell, suggesting extended deposition (Fig. 4; Moreno-Azanza *et al.* 2013; Grellet-Tinner *et al.* 2017; Choi *et al.* 2019*a*). In contrast, ornamentation of '*Stillatuberoolithus*' and modern emu eggshells is initiated in the middle of the eggshell with wedge-shaped structures (Fig. 6E,F; Oser 2018), implying another pathway of ornamentation construction. In *Gekko gecko* eggshell, ornamentation is composed of randomly oriented calcite grains and contains non-crystalline material inside (Choi *et al.* 2018). The three different crystallographical patterns of ornamentation indicate homoplastic ornamentation evolution. Phylogenetic occurrences of smooth maniraptoran eggshells are indicated with grey branches. Instances of morphological similarity that can be interpreted as clear convergent evolution and possibly other types of homoplasy are marked with solid and dashed arrows, respectively. Note that only convergent evolution is clearly detectable on crystallographic electron backscatter diffraction analysis. Silhouettes are attributable to (http://www.phylopic.org): Emily Willoughby (*Citipati*); Scott Hartman (*Archaeopteryx*), Darren Naish and Michael Keesey (*Dromaius*). Silhouettes of *Gekko*, *Caiman*, hadrosaur, sauropod and *Megapodius*, SD.

In the case of the ornamentation of '*Stillatuberoolithus*', it is underlain by a profoundly different generative mechanism from that seen in the typical two- or three-layered maniraptoran eggshells (Zelenitsky & Modesto 2003; Grellet-Tinner 2006; Lawver & Boyd 2018; Oser 2018), one also typified by *Pseudogeckoolithus* as we have shown. Accordingly, '*Stillatuberoolithus*' documents the emergence of a second ornamentation-building pathway in maniraptoran eggshell evolution. The presence of these two widely divergent building patterns shows that even if the dispersituberculate ornamentation of '*Stillatuberoolithus*' is extremely similar to that of *Pseudogeckoolithus*, this gross similarity clearly represents a case of convergent morphology. Similar instances of independent evolutionary acquisition and disappearance of closely comparable character states were also suggested in another eggshell component, the cuticle (D'Alba *et al.* 2016). In fact, calcified eggshell thickening per se has most likely evolved in diverse amniote clades, even within Dinosauria, several times independently (Stein *et al.* 2019).

The susceptibility of ornamentation to homoplasy has important implications for eggshell parataxonomy. It was argued that many eggshell characters are highly modular (*sensu* Klingenberg 2008) and are driven by mosaic evolution resulting in independent character combinations (Varricchio & Jackson 2004; Jackson *et al.* 2013; Lawver & Boyd 2018). The morphology of ornamentation is diverse in dinosaurian eggshells (Mikhailov 1997*a*), but we document here that even markedly different microstructure and crystallography can result in (or generate) almost identical gross morphologies, as shown in the cases of '*Stillatuberoolithus*' and *Pseudogeckoolithus* (Fig. 8).

For these reasons, we suggest that both morphology and its underlying crystallography (which can be used as a proxy of the eggshell calcite growth mechanism; see Choi *et al.* 2019*b*, text S6) have to be considered together before using superficial similarities as diagnostic eggshell characters implying homology in parataxonomical assessments. 30 However, there is still difficulty even in such mechanism-based identifications. Although EBSD can be used to identify definitive cases of convergent evolution in eggshell formation, characterized by different underlying mechanisms on crystallography, the reverse does not necessarily hold true: detecting the presence of a uniform mechanism does not always guarantee homologous origin of a feature, especially if the taxa of interest are only distantly related (see also Hall 2003; Shubin *et al.* 2009 for a more complicated case called 'deep homology'). Considering the limited number of possible ways to build ornamentation or even a hard eggshell per se (Stein *et al.* 2019), we may expect to find identical crystallography expressed in distantly related clades that nevertheless acquired (or re-invented) their common traits independently. So far, none of the known approaches in eggshell research has provided a way to safely separate true homology from homoplasy if a character shared by several taxa has both similar morphology and a similar underlying mechanism. Such difficulties notwithstanding, in the effort to establish monophyletic groups in eggshell parataxonomy, clearly convergent characters (such as the ornamentation in *G. gecko* eggshells and *Pseudogeckoolithus*, as demonstrated in this study) have to be identified, and handled accordingly (for further criticism on current practices in parataxonomy see also Zelenitsky *et al.* 2002; Varricchio & Jackson 2004; Grellet-Tinner 2006; but see Mikhailov 2014 for a contrary opinion). Only such rigorous approaches to phylogenetic analysis will make parataxonomic classification of the diverse fossil eggshell record a biologically and evolutionarily meaningful effort.

## SYSTEMATIC PALAEONTOLOGY

### Oofamily PRISMATOOLITHIDAE Hirsch, 1994 emend. Moreno-Azanza *et al.* 2014*b*

### Oogenus PSEUDOGECKOOLITHUS Vianey-Liaud & Lopez-Martinez 1997

*Type oospecies. Pseudogeckoolithus nodosus* Vianey-Liaud & Lopez-Martinez 1997.

*Emended diagnosis.* After Vianey-Liaud & Garcia (2003). Thin prismatic eggshell (200–350 μm including ornamentation), outer surface with dispersituberculate ornamentation, formed by irregular nodes, which are tubercle- or crater-like in shape. Wide pore openings at the top of some nodes. Egg shape and size unknown.

*Age and distribution.* Late Late Cretaceous (late Santonian – late Maastrichtian); upper Santonian – Maastrichtian of Europe (France, Hungary, Romania and Spain) and Maastrichtian of Africa (Morocco).

*Remarks.* The type material of *Pseudogeckoolithus*, supposedly housed at Universidad Complutense de Madrid, is currently not accessible because it was lost after the death of Professor López-Martínez. Future studies should consider collecting new material at Fontllonga 6 locality (Lleida, Spain) in order to establish a neotype for the oogenus.

### *Pseudogeckoolithus* cf. *nodosus*

Figures 3C, E; 4C, E; 5C, E

*Holotype and type locality.* FLL6-14, a single eggshell fragment from the early Maastrichtian Fontllonga 6 locality, Lleida, Spain (Vianey-Liaud & Lopez-Martinez 1997). The holotype material is lost.

*Distribution and age.* Vălioara-Fântânele, Densuș-Ciula Formation, Romania; early Maastrichtian; Blasi 2, Arén Formation, Spain; late Maastrichtian.

*Description.* Isolated eggshell fragments, 350 µm in thickness including ornamentation (280 µm excluding ornamentation). Outer surface with dispersituberculate ornamentation, with sparse nodes, sometimes with pore openings on the top of the nodes. In radial section, the eggshells show dinosaur prismatic morphotype, with a mammillary : continuous layer ratio of 1/3 to 1/9.

*Remarks.* We choose to use open nomenclature because the samples are too scarce, and we were not able to directly compare them with the holotype. Nevertheless, the proximity of Blasi 2 site to the roughly contemporaneous Fontllonga 6 type locality strongly supports attribution of *Pseudogeckoolithus* material from here to this oospecies.

### *Pseudogeckoolithus* aff. *tirboulensis*

Figures 3A, B, D; 4A, B, D; 5A, B, D

31 *Holotype and type locality.* ACH2-330, a thin section of an eggshell fragment; the Maastrichtian locality Achlouj 2, Morocco (Vianey-Liaud & Garcia 2003).

*Distribution and age.* Iharkút SZ-6 and SZ-7-8, Csehbánya Formation, Hungary; late Santonian; Petrești-Black Lens, Sebeș Formation, Romania, latest Campanian; Pui-Classic, Pui Beds, Romania, early late Maastrichtian.

*Description.* Eggshells are very thin (200–250 µm including ornamentation; 130–220 µm excluding ornamentation). Outer surfaces with dispersituberculate ornamentation, but somewhat more densely ornamented than *Pseudogeckoolithus* cf. *nodosus*. Pore openings on the top of some of the nodes. In radial section, they present dinosaur prismatic morphotype, with a mammillary : continuous layer ratio of 1:1 to 1:6.

*Remarks.* Eggshells referred in this study to *Pseudogeckoolithus* aff. *tirboulensis* resemble those described by Vianey-Liaud & Garcia (2003) from the Upper Cretaceous of Morocco in thickness, ornamentation and general histological structure. Nevertheless, they differ from the type material of *Pseudogeckoolithus tirboulensis* in the mammillary : continuous layer ratio, which in the African material is much higher (1:2). Accordingly, the *Pseudogeckoolithus* material from Hungary (see also Prondvai *et al.* 2017), and most probably that described here from the Romanian localities of Petrești-Black Lens and Pui-Classic, may represent a new oospecies of *Pseudogeckoolithus*.

## CONCLUSIONS

The contentious affinity of enigmatic ‘geckoid’ eggshells from Upper Cretaceous deposits of Europe was resolved: they were identified as theropod eggshells using a crystallographic approach (EBSD). This study provides a template case to enable potential squamate eggshells, a poorly investigated category in vertebrate palaeontology, to be rigorously tested and positively identified using EBSD. More importantly, we show that among nodular sauropsid eggshells, there are at least three different mechanisms that generate ornamentation (as shown on crystallography). Until recently, when a certain eggshell phenotype (=character) was found to share similar morphology across several taxa, these were usually treated as homologies, and were coded into the character–taxon matrix accordingly. However, similar morphology does not always represent homology, and may be homoplastic instead. Using a crystallographic approach, such hidden homoplasies (especially convergence) can be detected in the case of fossil and modern eggshells. Hence, before identifying a particular morphological similarity as a potential homology, its underlying mechanism should also be considered, in order to avoid treating homoplasy as homology. Finally, detailed crystallographic investigation of a more extensive sample of dinosaur (including Aves) and squamate eggshells is necessary, given that the present results point to a more complicated evolutionary history of the sauropsid eggshell crystallography (and also that of its production mechanisms) than was previously thought, with significant implications for the reconstruction of the reproductive (palaeo)biology of amniotes.

*Acknowledgements.* Seokyoung Han (Seoul National University) helped SC in constructing lower hemisphere pole figures. We also thank Gerald Grellet-Tinner (CRILAR/CONICET, Orcas Island Historical Museum), Mark Hauber (University of Illinois at Urbana-Champaign), Juan Daza (Sam Houston State University) and Rebecca Harris (Arizona State University) for confirming the contents in their papers and a book. 32 Kohei Tanaka (University of Tsukuba) and Noe-Heon Kim (SNU) helped us with the literature search. For help with specimens and information, we thank the following colleagues: Attila Ősi (Eötvös Loránd University) for collecting the Hungarian fossil eggshells; the Hungarian National History Museum and its chief curator for Paleontology and Geology, Alfréd Dulai, for access to fossil eggshells; Mátyás Vremir (Transylvanian Museum Society) for offering access to the Petrești-Black Lens eggshells, and sharing information concerning the Transylvanian enantiornithine eggshells; Ștefan Vasile (University of Bucharest) for helping to collect the Romanian specimens; José Ignacio Canudo (Director, Museo de Ciencias Naturales de la Universidad de Zaragoza) for providing access to Spanish specimens; Delphine Angst (University of Bristol) for contributing French thin-shelled eggshell specimens useful in comparisons; Eric Buffetaut (CNRS) for sharing information and providing references on French ‘geckoid’ eggshell occurrences; and Hiroki Echizenya (Hokkaido University Museum) and Kohei Tanaka for providing modern crocodylian eggshells. We appreciate Daniel Lawver (Stony Brook University), an anonymous referee and editors Imran Rahman and Sally Thomas for their constructive comments that helped to improve the previous version of this MS. Silhouettes in Figures 7 and 8 are attributed to Emily Willoughby (*Citipati*, CC-BY-SA 3.0), Scott Hartman (*Archaeopteryx*, CC0 1.0), and Darren Naish and T. Michael Keesey (*Dromaius*, CC-BY 3.0). This work was supported by National Research Foundation of Korea (grant number 2019R1A2B5B02070240) to YNL. MMA is supported by Fundação para a Ciência e a Tecnologia (project number PTDC/CTA-PAL/31656/2017 and postdoctoral grant number SFRH/BPD/113130/2015). EP was supported by the Bijzonders Onderzoeksfonds (BOF) – Universiteit Gent (grant number 01P12815); MTA-MTM-ELTE Research Group for Paleontology (grant number MTA-MTM-ELTE Paleo Contribution No. XXXX). 33

## AUTHOR CONTRIBUTIONS

SC and EP conceived the study. SC, EP and YNL designed the study. MMA, ZCS and EP provided fossil material and SC and YNL provided modern eggshells. SC performed analysis and collected data. All authors interpreted results. SC, MMA, ZCS and EP wrote the manuscript. All authors gave final approval for publication.

## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.v75qf08

*Editor*. Imran Rahman

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