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Fluorescent colour patterns in the basal pectinid *Pleuronectites* from the Middle Triassic of Central Europe: origin, fate and taxonomic implications of fluorescence

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Abstract: UV light-induced fluorescence is widely used as a key to reveal residual shell colour patterns of Neogene and Palaeogene molluscs. However, only few examples of fluorescent colour patterns are known from Mesozoic marine shells and little is known about the nature of fluorescence in fossils. Here, UV light-induced fluorescence reveals previously unseen abundance and diversity in the colour patterns of the basal pectinid *Pleuronectites laevigatus* from the Middle Triassic Muschelkalk of Central Europe. In addition to known variations of radial bands, a multitude of zigzag and zigzag-related patterns was found. The diversity of colour patterns is comparable to modern pectinids and is interpreted as colour pattern polymorphism. Raman spectra of the colour patterns indicated the preservation of residual organic pigments with aromatic moieties. The fluorescence properties of *P. laevigatus* and other basal pectinids from the Muschelkalk of Germany and France are described in detail, suggesting that colour pattern fluorescence is due to colourless diagenetic products of the pigments, not to the fossil pigments themselves. A remarkable feature of the colour patterns of *P. laevigatus* is the presence of different fluorescence colours. Because a gradual shift of the fluorescence colour from yellow to red with decreasing intensity to finally non-fluorescent is observed, which correlates with the provenance of the specimens, the fluorescence properties are interpreted to reflect differences in diagenetic history. The results show that the fluorescence colour of fossil molluscs, especially of Mesozoic molluscs, may be affected by diagenesis and should only be used with caution for taxonomic purposes.

Key words: Bivalvia, fluorescence, colour pattern, preservation, organic pigment, Muschelkalk.

Colour patterns are only occasionally preserved in fossil marine shells (Hollingworth & Barker 1991; Williams 2017). To reveal residual traces or to enhance visible colour patterns, ultraviolet (UV) light-induced fluorescence has been used, either using natural autofluorescence (Miethe & Born 1928; Rolfe 1965; Nuttall 1969; Neuffer 1971, 1972; Psarras *et al.* 2021) or fluorescence observed following treatment of the shells with chlorine bleach (e.g. Vokes & Vokes 1968; Krueger 1974). The latter technique in particular has been widely used for Neogene and Palaeogene molluscs, mainly for gastropods but also for bivalves (Dockery 1980; Swann & Kelley 1985; Gorka 2008; Merle *et al.* 2008; Caze *et al.* 2010, 2011*a*, 2011*b*; Hendricks 2015, 2018; Pacaud & Sautereau 2020). However, only a few examples of fluorescence have been reported for Mesozoic marine shells and no examples are known from the Palaeozoic. Miethe & Born (1928) briefly described fluorescent colour patterns of a Cretaceous oyster, a Jurassic ammonite and a Triassic pectinid. More recently, Caze *et al.* (2015) reported residual colour patterns in gastropods and bivalves with exceptional preservation of aragonitic shells from the Jurassic Cordebugle Lagerstätte (Calvados, France).

The Triassic pectinid specimen mentioned by Miethe & Born (1928) has not been figured, but is of special interest, because it represents by far the oldest example of any fluorescent colour pattern. It has been described as convex valve of *Pecten* from the Nodosenkalk of Bindlacher Berg near Bayreuth (Germany) showing orange-red radially split bands under UV light. From the description, it is most likely that it was a specimen of *Pleuronectites laevigatus*, a common pectinid from the Middle Triassic Muschelkalk. This taxon represents the geologically oldest species of scallops in the strict sense (i.e. Pectinidae) (Hautmann 2010) and the preservation of colour patterns of this species has been well known since the nineteenth century (Goldfuss 1834–1840), having been figured and described many times since then (e.g. Seebach 1861;

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Grabenhorst & Mundlos 1987; Gensel *et al.* 1990). Typically, colour patterns occur on the left (upper) valve and consist of radial bands or bundles of bands, although less common radial bands are also found on the right valve (Hagdorn 1995). In addition to radial bands, Fischer (1925) and Hagdorn (1995) described two further but less common types of colour pattern: zigzag patterns (var. *derognati*) and concentric colour bands (var. *zonata*). However, except for the early mention of a putative *P. laevigatus* by Miethe & Born (1928), the potential for the colour patterns of *P. laevigatus* to show fluorescence under UV light has been overlooked.

Here, based on a comprehensive sample set, the fluorescence properties of *P. laevigatus* and other basal pectinids from the Middle Triassic Muschelkalk are analysed in detail, in order to reveal the abundance and diversity of their colour patterns and to explore the general nature of colour pattern fluorescence.

MATERIAL AND METHOD

For the present study, 120 specimens of *P. laevigatus* Schlotheim, 1820, from the Upper Muschelkalk, with preserved colour patterns (out of several hundred without colouration) were investigated. All specimens, ranging from juveniles to adults, are consistent with previous descriptions of the species and include originals of Schlotheim (1820), Goldfuss (1834–1840), Seebach (1861) and Hagdorn (1995). The studied specimens with colour patterns are listed in Appendix S1 and are stored in the Bayerische Staatssammlung für Paläontologie & Geologie (BSPG), the Geologisch-Paläontologisches Institut der Universität Heidelberg (GPIH), the Institut für Geowissenschaften der Universität Tübingen (GPIT), the Geowissenschaftliches Zentrum der Universität Göttingen (GZG), the Institut für Paläontologie der Universität Bonn (IPB), the Museum für Naturkunde Berlin (MB), the Muschelkalkmuseum Hagdorn Ingelfingen (MHI), the Naturhistorisches Museum Heilbronn (NHMH), the Naturhistorisches Museum Schloss Bertholdsburg Schleusingen (NHMS), the Naturkundemuseum im Ottoneum Kassel (NMOK), the Staatliches Museum für Naturkunde Stuttgart (SMNS), the Staatliches Naturhistorisches Museum Braunschweig (SNHM) and the Sammlung Mainfränkische Trias Euerdorf (SMTE). In addition, the fluorescence properties of further pectinids from the Muschelkalk (MHI, NHMS and SMNS) and of modern pectinids based on the malacological collection of the SMNS were surveyed.

UV light-induced autofluorescence was documented using a Canon PowerShot A700 digital camera and a Philips TDL 18W/08 UV-A blacklight blue lamp (340–400 nm, emission maximum at 365 nm), with a distance from the light source to the fossils of about 10 cm. The exposure time for all UV photographs was four seconds. Any coatings of varnish, if present, were removed with acetone before documentation. In contrast to previous studies (e.g. Caze *et al.* 2015) no chemical treatment with chlorine bleach was applied to enhance the natural fluorescence of the colour patterns, because such treatment would irreversibly change the original composition of the preserved organic material.

For non-destructive characterization of the pigments of *P. laevigatus*, several specimens with preserved colour patterns (showing yellowish orange to reddish orange fluorescence in UV light) were cleaned with acetone and subjected to *in situ* Raman spectroscopy: GZG.INV.12130 (radial bands), GZG.INV.14919 (zigzag pattern), GZG.INV.14924 (radial bands) and GZG.INV.45639 (radial bands). Raman measurements of pigmented and unpigmented areas of the exterior shell surface were performed using a Horiba Labram HR800 UV instrument equipped with an Olympus BX41 microscope. The excitation wavelength was the 488 nm line of a diode laser with a reduced laser power of about 0.45 mW at the sample surface to avoid any sample deterioration. The use of a 100× objective for focusing the laser on the sample surface and a confocal hole of 100 µm yielded a spatial resolution of about 1 µm lateral and 5 µm in depth. The scattered light was dispersed by a grating with 600 lines mm^{-1} and detected with a charge-coupled device (CCD) detector. Raman spectra were acquired in the range of 100–2100 cm^{-1} and final spectra were averaged from 4 or 8 spectra with 30 s exposure time each. The spectrometer was calibrated against the Si band at 520.4 cm^{-1} and the Horiba intensity correction system (ICS) was applied to minimize interference effects of the edge filters that may occur in samples with high fluorescence.

RESULTS

Colour patterns observed in natural light

Because only the calcitic outer ostracum is preserved from the original shell of *P. laevigatus* (Hagdorn 1995), colour patterns can be observed both in specimens that show the exterior and those that show the interior of the shell. The colour patterns appear to differ in their shades of brown, ranging from light brown to reddish brown to almost black, depending on the specimen. However, in fact, there are almost no differences in the colour of the patterns, since the shell is very thin (0.25–0.4 mm according to Carter & Hautmann 2011) and translucent, and therefore the brown colour of the patterns is strongly influenced by the colour of the underlying sediment matrix. This is

most obvious when the shell can be separated from the sediment. Thus, colour patterns of specimens imbedded in a light grey limestone appear light brown in colour (e.g. specimen GZG.INV.45639), whereas those of specimens imbedded in a dark grey limestone appear almost black in colour (e.g. specimen GPIH K.4082) (see Fig. S1).

Although not discussed further in this work, it should be noted that pigmented portions of the shell of *P. laevigatus* and other fossil shells from the Muschelkalk have a lower solubility during diagenetic pressure solution than unpigmented portions, which may result in colour patterns being transformed into 'pseudosculptures' (Haggdorn 1995). Different stages (predominantly very early stages) of 'pseudosculpture' can also be observed in some of the specimens in the present study.

Fluorescence of colour patterns

The majority of colour patterns of *P. laevigatus* display a distinct fluorescence under long-wave UV light (under short-wave UV light the fluorescence intensity is lower). By using UV light, colour patterns can be significantly enhanced and thus colour patterns that are weak or obscure under normal light conditions can be revealed (Fig. 1). This is exemplified by the *P. laevigatus* specimen shown in Figure 1A, B. Under normal light, it shows radial colour bands in the central part of the shell but uniform colouration after a growth disruption. Under UV light, however, a continuation of the colour bands beyond the growth disruption is revealed. Especially zigzag patterns that are often very difficult to recognize, can be easily detected with UV light (Fig. 1C, D). This way, numerous variations of zigzag pattern were found in addition to radial lines and bands, ranging from patterns composed of individual zigzag elements such as chevrons (Fig. 2A) to zigzag and flamed patterns (Fig. 2B) up to diffuse zigzag patterns to uniform coloured shells (Fig. 2C). The course of zigzag and flame patterns often rises from the edges to the centre of the shell towards the umbo (Fig. 2). Some specimens show even more complex patterns composed of first and second order patterns (Figs 2D–G, 3A) including first order radial patterns combined with second order zigzag patterns (Fig. 2D, E). Surprisingly, no concentric patterns were observed. In some specimens it can also be observed that colour patterns are more pronounced in the juvenile stage and disappear to some extent after a growth disruption (e.g. Fig. 1A, B). Some slabs with several specimens of *P. laevigatus* show that colour patterns occurred abundantly at least locally (Fig. 3) and specimens with radial bands and zigzag patterns occurred at the same time and the same locality (Fig. 3A). In total, about 20% of the studied *P. laevigatus* specimens with colour patterns reveal zigzag or zigzag-related patterns. The actual amount, however, is very likely to be even higher, since zigzag patterns, compared to the more conspicuous radial patterns, have often been overlooked in the field and are therefore underrepresented in collections. Based on the analysed specimens, originating from different horizons from the Trochitenbank 1 up to the Upper Terebratelbank, colour pattern variations are independent of the stratigraphic level and occur throughout the Upper Muschelkalk (Appendix S1). Furthermore, no obvious biogeographic trend in the occurrence of specific colour patterns was found.

Regional differences of colour pattern fluorescence

The colour patterns of *P. laevigatus* show different fluorescence colours, ranging from yellow to orange to red, comprising all transition colours (Fig. 4). Fluorescence intensity generally decreases from yellow to red to non-fluorescent specimens (Fig. 4), apart from individual differences related to varying pigment concentrations (Fig. 1B). The fluorescence properties are similar for *P. laevigatus* specimens from a specific locality, but vary considerably depending on their provenance (Fig. 5; Appendix S1). Specimens from northern Germany (Figs 2C, D, 4A), the area of Bayreuth (Figs 1D, 4B) and from north-eastern France (Lorraine) typically show a yellow to orange fluorescence, whereas specimens from north-east Baden-Württemberg rather exhibit an orange to red fluorescence (Figs 1B, 3, 4C). Specimens from the north-west part of Baden-Württemberg even show no fluorescence at all (Fig. 4D). These differences in the colour of fluorescence can be correlated with neither the type of colour pattern nor the stratigraphic level.

Further pectinids with fluorescent colour patterns

In addition to *P. laevigatus*, fluorescent colour patterns can also be observed in the pectinid *Entolium*. Specimens of *Entolium* cf. *tenuistriatum*, from the Lower Muschelkalk of Rüdersdorf near Berlin, occasionally show a delicate colour pattern consisting of fine radial to divaricate brown lines, which show an intense yellow fluorescence under UV light (Fig. 6A, B). A similar colour pattern of an *Entolium* cf. *discites* from the Upper Muschelkalk from Troistedt near Weimar showed orange fluorescence (Fig. 6C, D). Broad fluorescent bands were observed in a specimen of *Leptochondria albertii* from the Upper Muschelkalk of Bindlach near Bayreuth (Fig. 6E, F). However, in contrast to other fossils, the colour pattern of *L. albertii* was only visible using UV light.

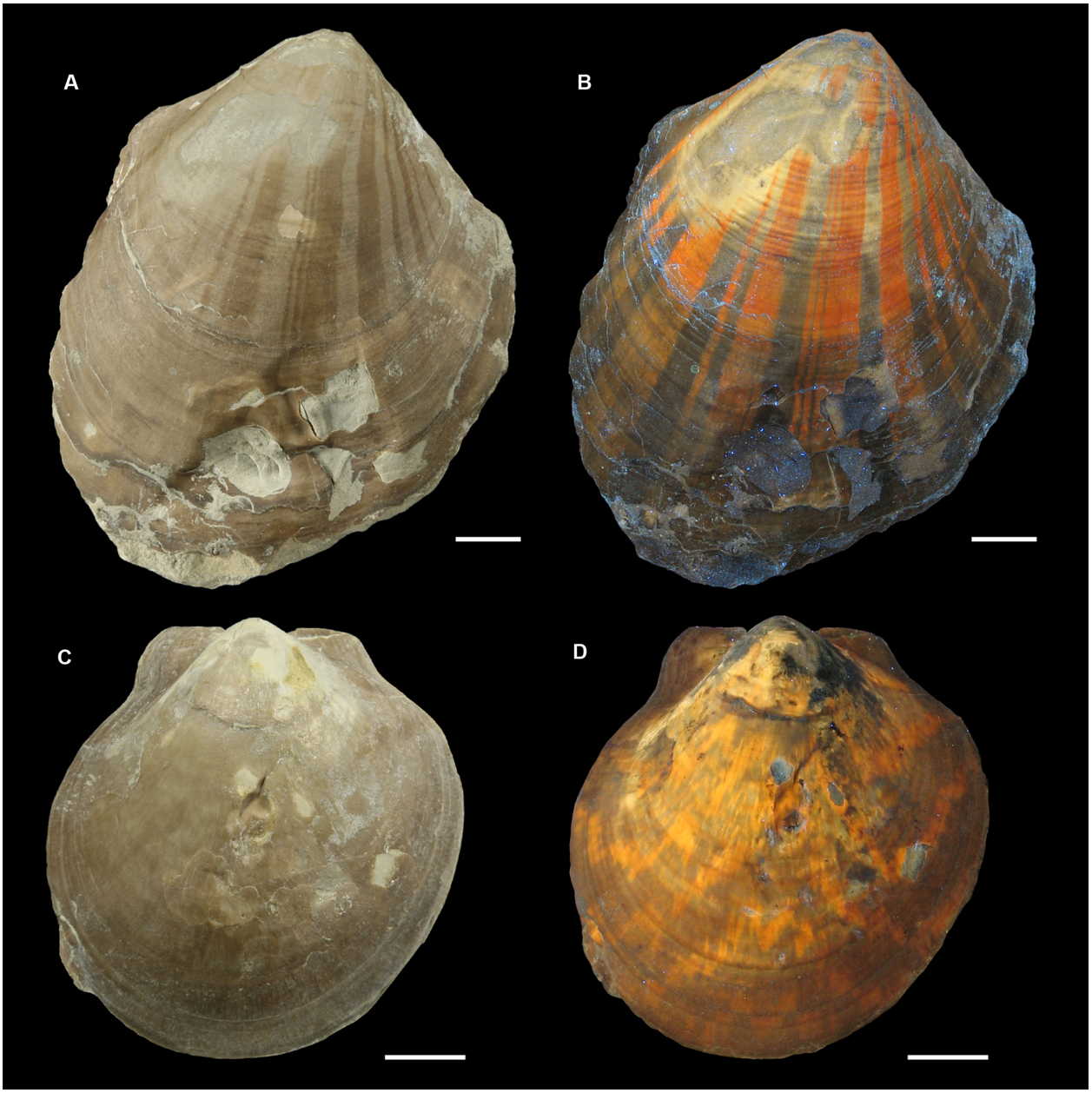
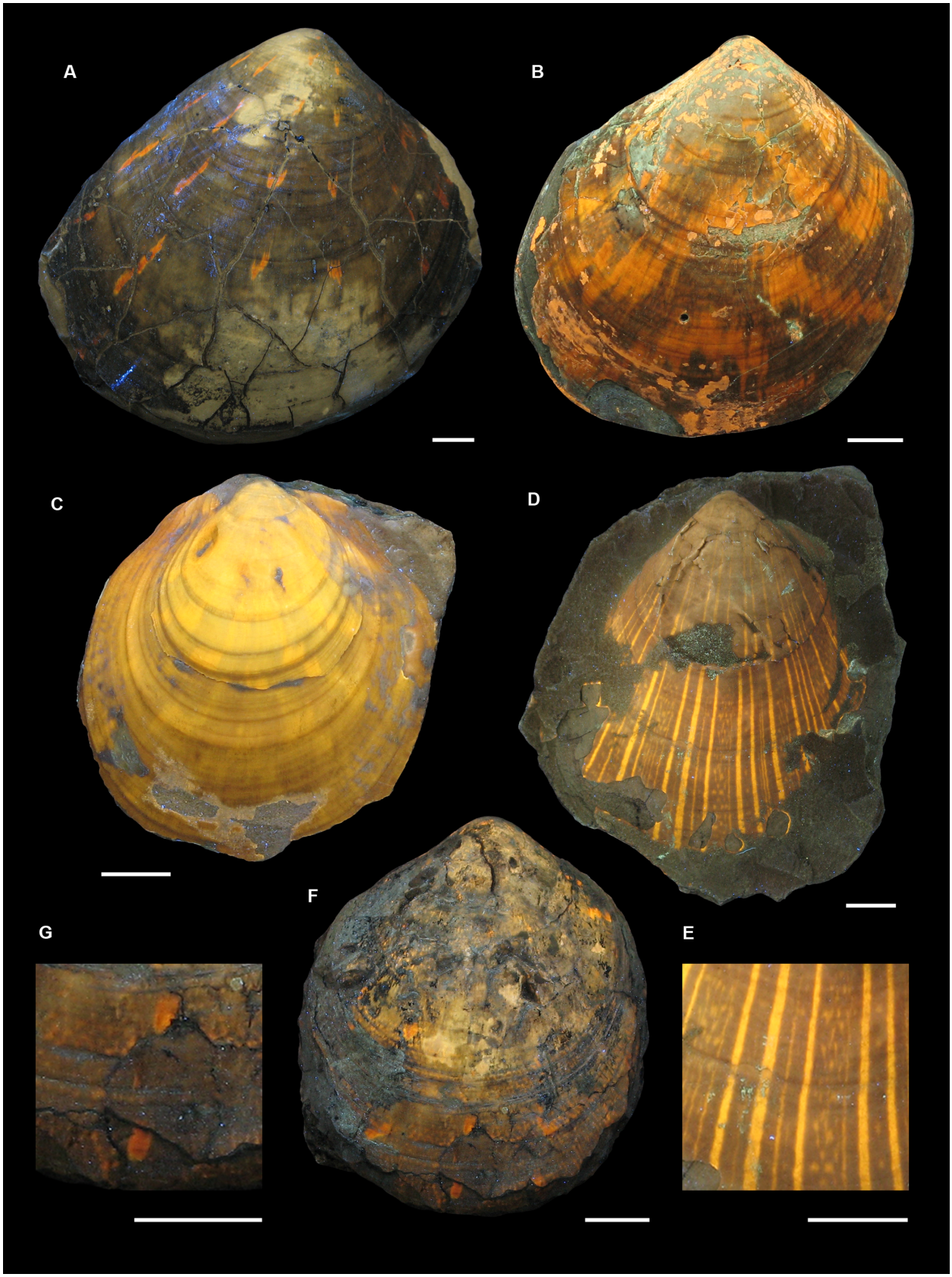


FIG. 1. UV light-induced fluorescence revealing residual colour patterns in *Pleuronectites laevigatus*. A–B, left valve with broad radial colour bands showing continuation of bands after a growth line only under UV light, Upper Muschelkalk, Trochitenkalk Formation, *robustus* Zone, Neidenfels near Crailsheim, Germany, MHI 2077/8. C–D, left valve with zigzag pattern, Upper Muschelkalk, Bindlach near Bayreuth, Germany, SMNS 75197-4. A, C, specimens under normal light; B, D, specimens under UV light. Note that in adult specimens of the species auricles are often not preserved. Scale bars represent 1 cm.

FIG. 2. Variability of colour patterns in *Pleuronectites laevigatus*. A, left valve with chevron pattern, Upper Muschelkalk, Meißner Formation, Nitzenhausen near Künzelsau, Germany, MHI 2077/16. B, left valve with zigzag pattern, Upper Muschelkalk, Hildesheim, Germany, GZG.INV.14919; note remains of coating material in depressions of the shell with similar fluorescence than colour pattern. C, left valve with diffuse zigzag pattern to almost uniform colouration, Upper Muschelkalk, Trochitenkalk Formation, Schöningen, Germany, SMNS 75371-2. D–E, left valve with complex first and second order colour pattern, Upper Muschelkalk, Schöningen, Germany, MB.M.6059; E, close up of colour pattern. F–G, left valve with complex first and second order colour pattern, Upper Muschelkalk, Trochitenkalk Formation, Bucha near Jena, Germany, SMNS 75372; G, close up of colour pattern. All specimens under UV light. Scale bars represent 1 cm.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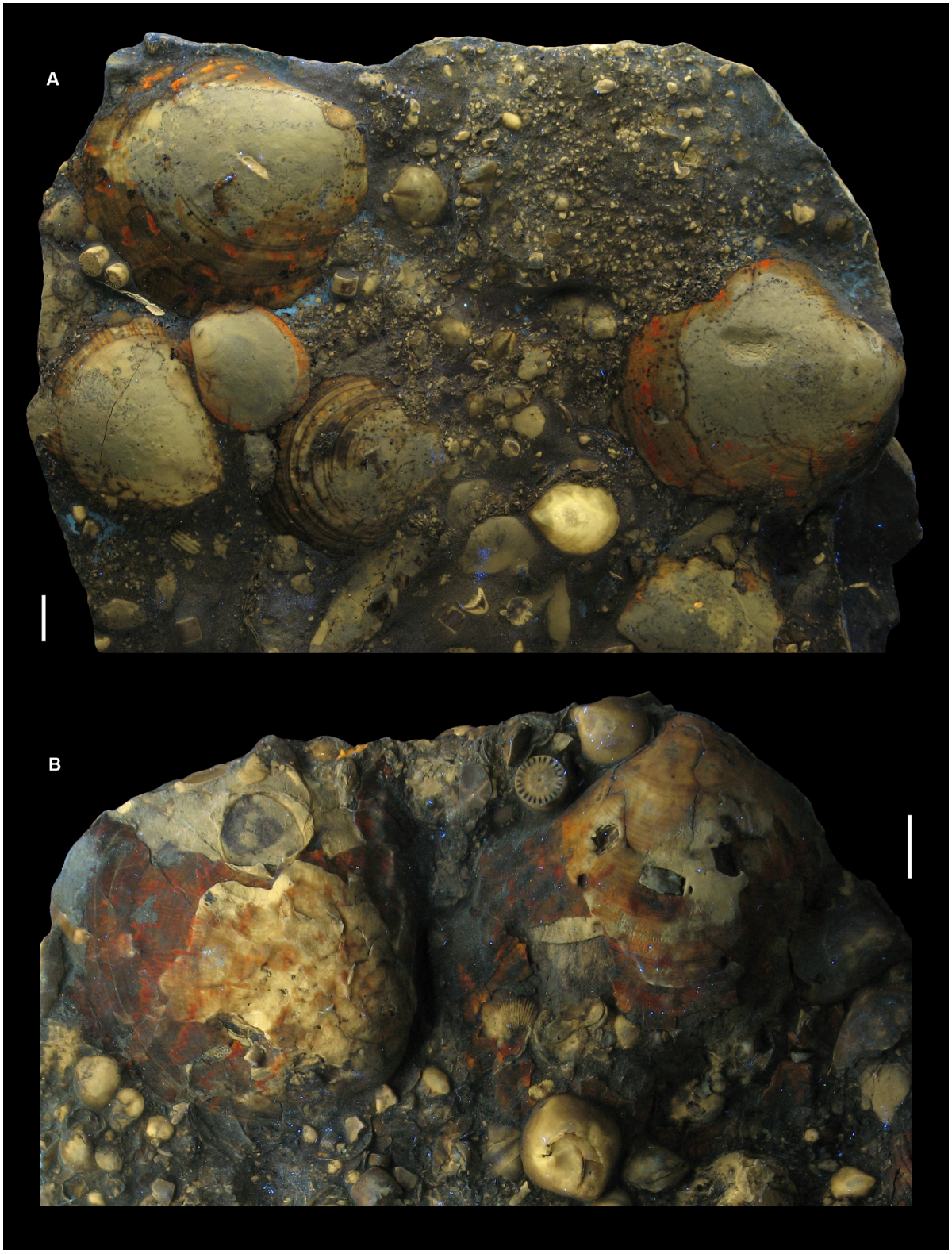


FIG. 3. Abundance of colour patterns in *Pleuronectites laevigatus*. A, assemblage of specimens with different types of colour patterns, Upper Muschelkalk, Trochitenkalk Formation, Mistlau near Kirchberg/Jagst, Germany, NHMH 411-161/2003. B, two left valves, Upper Muschelkalk, Trochitenkalk Formation, Schwäbisch Hall, Germany, SMNS 25358-1. All specimens under UV light. Scale bars represent 1 cm.

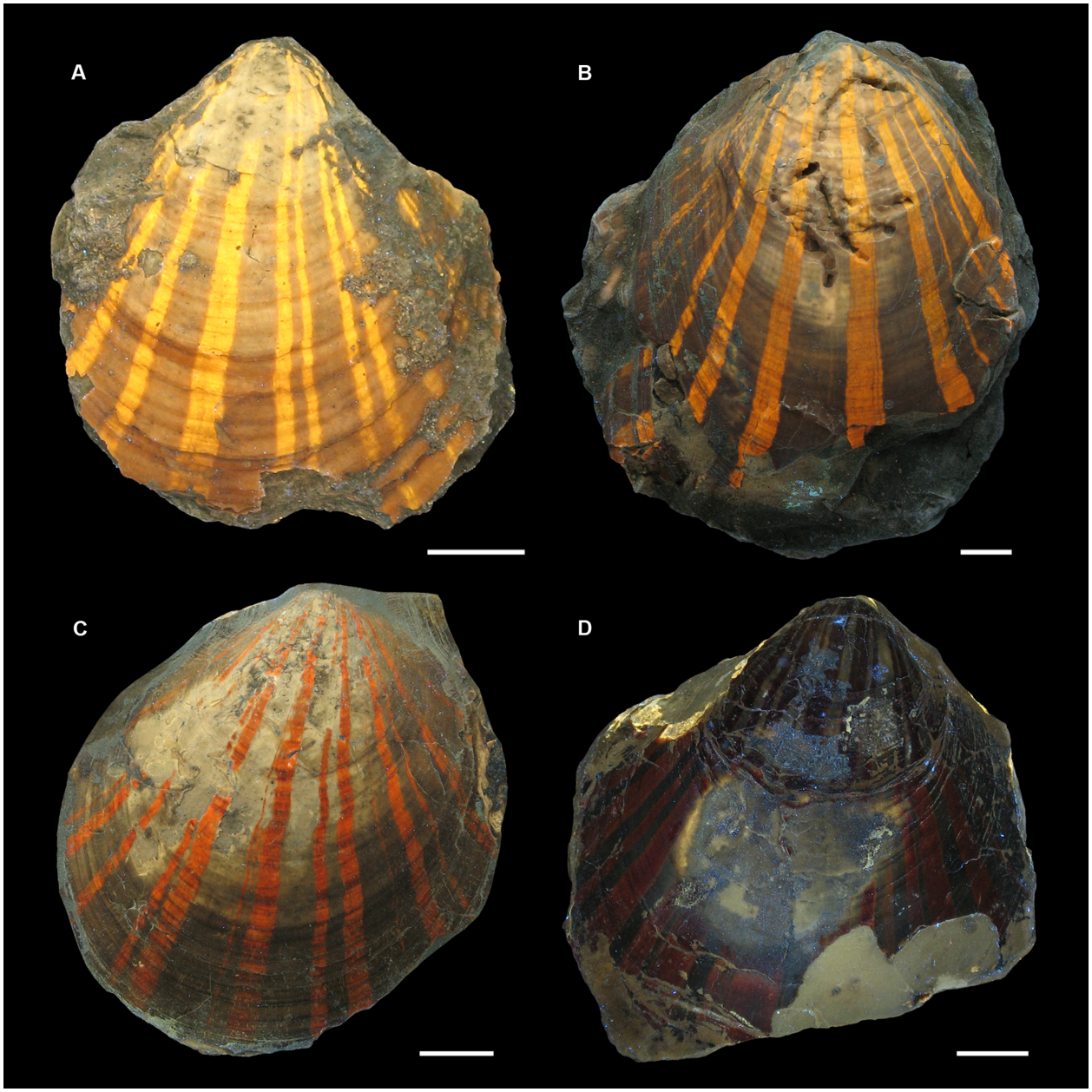


FIG. 4. Range of fluorescence colours in colour patterns of *Pleuronectites laevigatus*. A, left valve, Upper Muschelkalk, Wernigerode (locality 4 in Fig. 5), Germany, MB.M.6057. B, left valve, Upper Muschelkalk, Trochitenkalk Formation, Bindlach near Bayreuth (locality 13 in Fig. 5), Germany, SMNS 75197-1. C, left valve, Upper Muschelkalk, Trochitenkalk Formation, Gerabronn (locality 19 in Fig. 5), Germany, SMNS H 108-1. D, left valve, Upper Muschelkalk, Meißner Formation, Gundelsheim (locality 29 in Fig. 5), Germany, SMNS 75379. All specimens under UV light. Scale bars represent 1 cm.

Lack of fluorescence in modern pectinids

No fluorescence related to shell colour was observed in the numerous modern pectinid specimens of the malacological collection of the SMNS. Furthermore, despite the great variety of present-day pectinid species, showing a plethora of colours and colour patterns, no reports of corresponding fluorescence were found in the literature.

Raman analysis of pigments

All analysed specimen of *P. laevigatus* yielded Raman spectra with broad signals at about 1350 and 1600 cm^{-1} (Figs 7, S2), although a high background was observed due to yellowish orange to reddish orange autofluorescence. These signals were obtained mainly from the colour bands (radial bands and zigzag

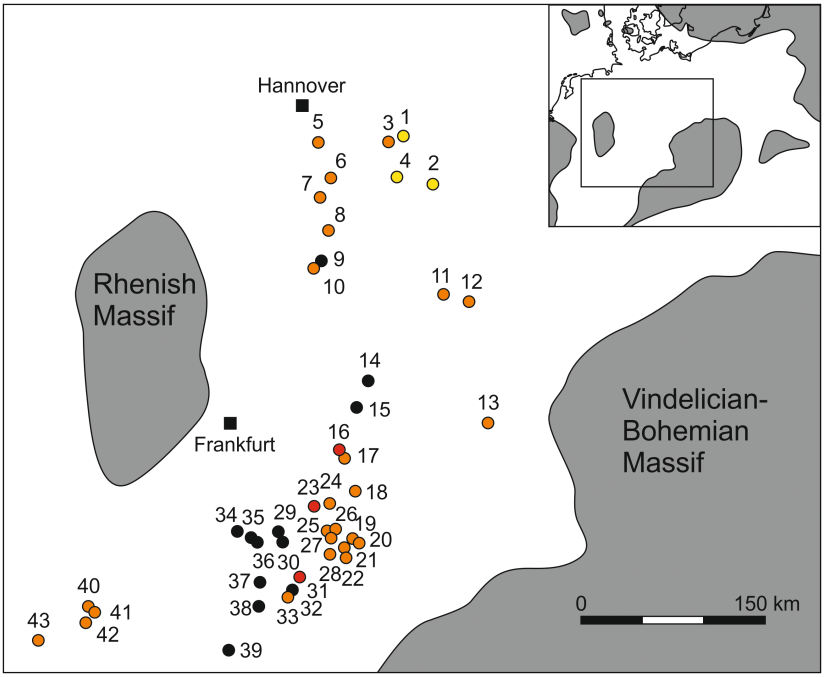


FIG. 5. Middle Triassic palaeogeography of Central Europe (Germanic Basin) with localities in Germany and north-eastern France that yielded *Pleuronectites laevigatus* specimens with preservation of colour patterns. The colour of the circles indicates the average fluorescence colour of the colour patterns at the localities; black circles indicate that colour patterns are non-fluorescent. 1, Schöningen; 2, Badeborn; 3, Uehrde; 4, Wernigerode; 5, Hildesheim; 6, Bad Gandersheim; 7, Iber; 8, Diemarden; 9, Großalmerode; 10, Hessisch Lichtenau; 11, Weimar; 12, Jena; 13, Bayreuth; 14, Hollstadt; 15, Schwarze Pfütze; 16, Güntersleben; 17, Würzburg; 18, Baldersheim; 19, Gerabronn, Kirchberg, Mistlau; 20, Crailsheim (Bölgental, Gaismühle, Wollmershausen, Neidenfels, Auhof); 21, Ilshofen; 22, Vellberg-Eschenau, Ummenhofen; 23, Schillingstadt; 24, Bad Mergentheim; 25, Künzelsau-Garnberg; 26, Nitzenhausen; 27, Kupferzell; 28, Schwäbisch Hall (Gottwollshausen, Steinbach, Tullau, Willhelmsglück); 29, Gundelsheim, Haßmersheim; 30, Bad Friedrichshall; 31, Zwingelhausen; 32, Neckarrems; 33, Stuttgart-Bad Cannstatt; 34, Nußloch; 35, Hoffenheim; 36, Steinsfurt; 37, Roßwag; 38, Malmsheim; 39, Schopfloch; 40, Bettborn; 41, Réding; 42, Héming; 43, Lunéville. Palaeogeography according to Ziegler (1982), modified from Hagdorn (1991).

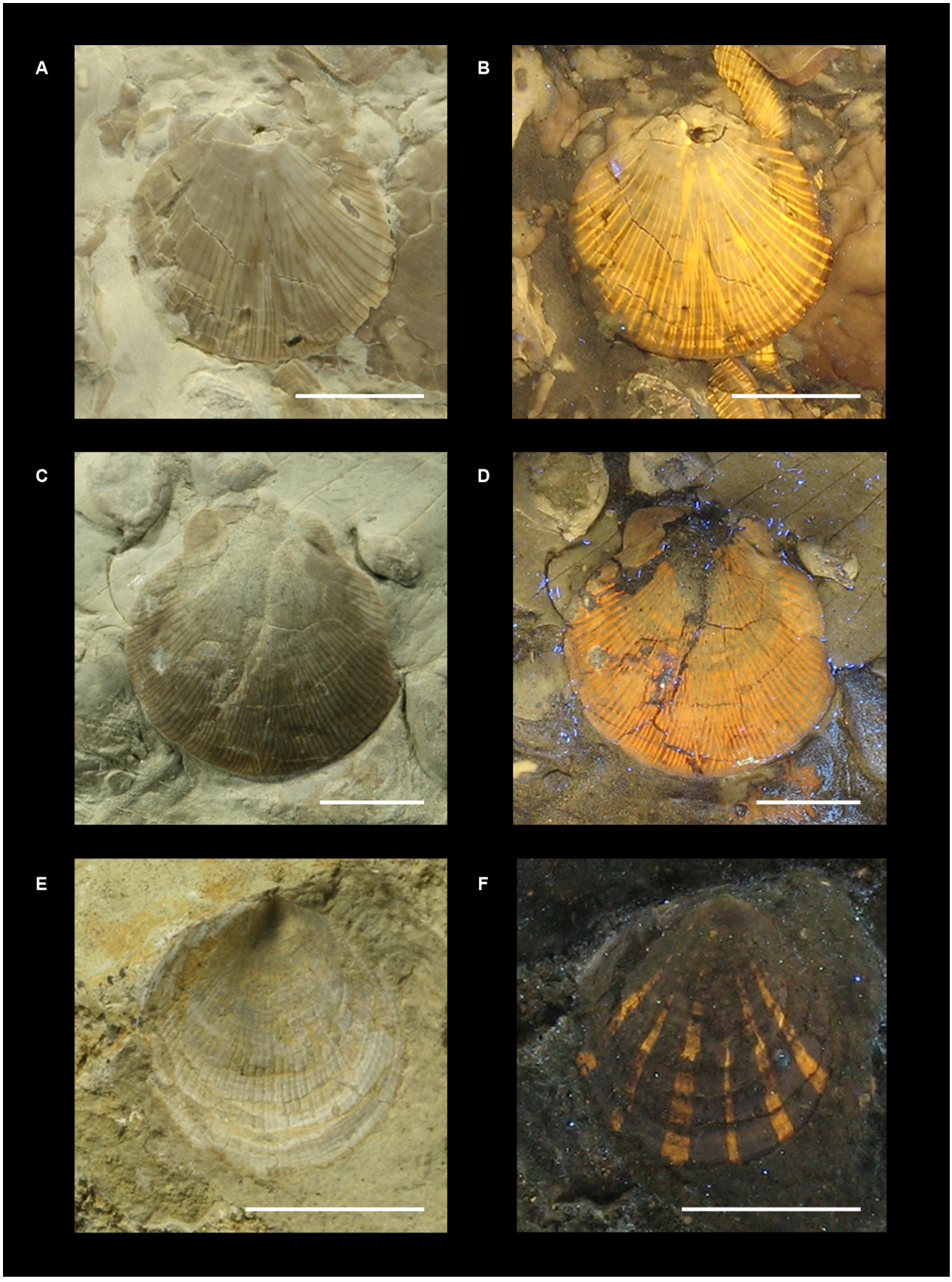
patterns), and with much lower intensity also from the colourless shell. No Raman signals were found that would indicate the presence of potentially staining iron oxides.

DISCUSSION

Abundance and diversity of colour patterns

UV light-induced fluorescence shows that colour patterns are much more abundant and diverse in *P. laevigatus* than previously known. This is especially the case for zigzag and zigzag-related patterns. A multitude of colour patterns is observed and the occurrence of numerous intermediate forms suggest that colour pattern variability represent phenotypic variations of a single species. The formation of such patterns and their diversity can be understood by reaction–diffusion processes as described for modern sea shells (Meinhardt 2009). Variations of colour patterns have also been observed in pectinids from the Oligocene of the Mainz Basin in Germany (e.g. *Chlamys picta*) (Neuffer 1972). The variability of colour patterns in *P. laevigatus* is comparable to modern pectinids and can be considered as colour pattern polymorphism. Polymorphism of both colour and pattern is well known

FIG. 6. Fluorescent colour patterns of further pectinids from the Muschelkalk. A–B, *Entolium* cf. *tenuistriatum*, Lower Muschelkalk, Rüdersdorf, Germany, MHI 2077/23. C–D, *Entolium* cf. *discites*, Upper Muschelkalk, Troistedt near Weimar, Germany, NHMS WT 1960. E–F, *Leptochondria albertii*, Upper Muschelkalk, Bindlach near Bayreuth, Germany, SMNS 75197-5. A, C, E, specimens under normal light; B, D, F, specimens under UV light. Scale bars represent 1 cm.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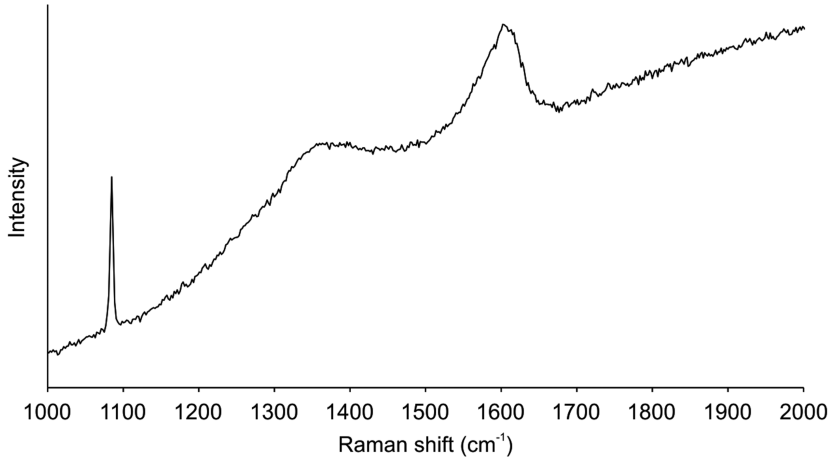

FIG. 7. Raman spectrum of brown colour band of *Pleuronectites laevigatus*, Upper Muschelkalk, Weimar, Germany, GZG.INV.12130. The signal with a Raman shift of 1085 cm^{-1} is due to calcite.

in many modern pectinids; in *Argopecten irradians* (Adamkewicz & Castagna 1988) and *Chlamys nobilis* (Yuan *et al.* 2012), for example. The observation that the left (upper) valve of various modern pectinid species (e.g. *Mizuhopecten yessoensis*, *Pecten maximus*) (Affenzeller *et al.* 2019) is more strongly coloured or more often coloured than their corresponding right (lower) valve suggests a functional importance of colour (patterns) in pectinids such as camouflage. Since in *Pleuronectites* disruptive colour patterns (radial bands, zigzag patterns) occur predominantly on the left valve, these patterns may have served as a camouflage as well (see also Hagdorn 1995).

Despite the diversity of colour patterns observed in *P. laevigatus*, no evidence for concentric colour bands (var. *zonata*) (Fischer 1925; Hagdorn 1995) was found. The previously depicted specimen MHI 1252/4, displaying radial and concentric colour bands when viewed under normal light (Hagdorn 1995, fig. 1e), shows only fluorescence of the radial colour bands, suggesting that only these bands represent the original colour pattern of the specimen. Selective dissolution of the shell along growth bands may have led to apparent concentric patterns in *P. laevigatus*.

It is striking that abundant occurrences of *P. laevigatus* specimens with preservation of colour patterns were mainly found near bivalve/crinoid bioherms, as the examples from Mistlau (Fig. 3A) and Schwäbisch Hall (Fig. 3B) show. Apparently, rapid burial and cementation contributed to the exceptional preservation of the colour patterns. A great variability of colour patterns was observed not only in general, but also at both of these localities (Fig. 3), indicating that variations in colour patterns were non-ecophenotypic.

Composition of colour pattern pigments

Until recently, surprisingly little was known about the pigments of modern molluscan shells (Williams 2017). Investigations based on Raman spectroscopy have suggested that the different colourations of modern pectinids are due to polyenes (a class of compounds including e.g. carotenoids) (Barnard & de Waal 2006; Hedegaard *et al.* 2006; Ishikawa *et al.* 2019; Wade *et al.* 2019), which show strong signals at about 1100 and 1500 cm^{-1}. However, Raman spectra of the colour bands of *Pleuronectites* do not show the characteristic and strong bands of polyenes, indicating that such pigments, if once present, are not preserved. Moreover, no signals of carotanes (i.e. diagenetically altered carotenoids; strong signal at 1455 cm^{-1}) that had suffered hydrogenation of the polyene chain (Marshall & Olcott Marshall 2010) were detected in the Raman spectra of *Pleuronectites*. Instead of these signals, the spectra show broad bands at about 1350 (D band) and 1600 cm^{-1} (G band) (Fig. 7), which are characteristic for (poly)aromatic structures (Olcott Marshall & Marshall 2015). The presence of such broad bands in Raman spectra suggests an overlap of individual bands, which would be observed for mixtures of compounds or macromolecular substances. Similar broad bands at about 1350 and 1600 cm^{-1} are also observed in Raman spectra of (eu)melanins (Pinheiro *et al.* 2019).

Since the early investigations of Comfort (1951), brown colouration in modern molluscan shells has been attributed to melanins. Because of the colour and the resistance of melanins, the pigments of brown fossil colour patterns have also been attributed to melanins (Hollingworth & Barker 1991). Dark coatings (e.g. black layer) are well known from cephalopods from the Muschelkalk (Klug

et al. 2004), and D and G bands suggesting melanin-like pigments were observed in the Raman spectrum of a black-banded shell of the terebratulid brachiopod *Coenothyris*, a common non-molluscan invertebrate from the Muschelkalk (Gaspard *et al.* 2019). However, investigations using Raman spectroscopy (Barnard & de Waal 2006; Hedegaard *et al.* 2006; Ishikawa *et al.* 2019; Wade *et al.* 2019) and mass spectrometry (Affenzeller *et al.* 2019, 2020) have shown that not all brownish pigments in the shells of modern molluscs consist of melanin. Because Raman spectra of structurally different compounds with polyaromatic moieties show D and G bands, currently without further chemical analysis no clear assignment to melanins can be made.

Based on the results from Raman spectroscopy, no indications of the presence of further organic pigments known from modern molluscs (e.g. porphyrins) were found in *Pleuronectites*.

Origin and fate of colour pattern fluorescence

The lack of fluorescence in the colour patterns of modern pectinids is in strong contrast to the distinct fluorescence in the patterns of fossil pectinids, indicating that the fluorescence observed in the latter is not an original feature. Similar fluorescence properties have been observed for specimens of the bivalve *Paphia* (Veneridae) (Nuttall 1969) and members of the Cyrenidae (Grimm 2020). Whereas modern specimens of these bivalves show no fluorescence of the colour patterns under UV light, the residual patterns of fossil representatives show strong fluorescence under the same conditions. A lack of fluorescence has also been reported for other modern molluscs such as neogastropods (Krueger 1974), although it should be noted that members of the Vetigastropoda and some other taxa are known that show a red fluorescence due to porphyrins (Comfort 1951; Williams 2017).

Remarkably, fluorescence of previously non-fluorescent residual colour patterns of fossil shells can be artificially generated by treatment with chlorine bleach as commonly applied in the literature (e.g. Krueger 1974; Caze *et al.* 2015), suggesting that oxidation of primary organic matter leads to fluorescent products. It is therefore likely that autofluorescence in colour patterns of most fossil molluscs is a secondary feature, emerging by natural alteration of the organic pigments during diagenesis. The example of the *Leptochondria albertii* specimen from the Upper Muschelkalk of Bindlach (Fig. 6E, F) with colour patterns only visible in UV light unequivocally shows that it is not the pigments themselves, but fluorescent products of the pigments that are the source of fluorescence. Colour patterns visible in UV light but not in normal light were also observed in one poorly preserved specimen of *P. laevigatus* from Stuttgart-Bad Cannstatt (SMNS 75384, specimen not shown; for further details see Appendix S1).

The fluorescence of fossil shell colour patterns is generally described as yellow to yellow-orange (e.g. Krueger 1974; Caze *et al.* 2011*a*). Only members of the Vetigastropoda from the Eocene of the Paris Basin (Merle *et al.* 2008; Caze *et al.* 2011*a*) and the Jurassic Cordebugle Lagerstätte (Calvados, France) (Caze *et al.* 2015) have been described to emit red fluorescence, which has led the authors to conclude that the fluorescence colour may be used for systematic purposes. Recently, Grimm (2020) suggested that the yellow fluorescence of fossil bivalves may be due to degradation products of carotenoids. However, the stability of carotenoid pigments is not very high, and as shown above, neither the preservation of polyene pigments nor the occurrence of geological stable carotanes is supported for *Pleuronectites*. The polyaromatic signature observed in the Raman spectra of *Pleuronectites* may be only explained by polyene compounds that experienced a very high degree of cyclization and aromatization of the polyene chain (Sinninghe Damsté & Koopmans 1997). Melanin pigments are known for their stability, but show no fluorescence. However, oxidation products of melanin are well known for their intense yellow fluorescence (Kayatz *et al.* 2001). Although melanin pigments are less common in molluscan shells than previously believed (Affenzeller *et al.* 2019, 2020), it is possible that the fluorescence of *Pleuronectites* is due to degradation products of melanin or other stable macromolecular pigments.

A remarkable feature of the colour patterns of *P. laevigatus* is the presence of different fluorescence colours, ranging from yellow to red, within one species (Fig. 4). Because the fluorescence intensity decreases from yellow to red to finally non-fluorescent, and these differences in the fluorescence are specific to the region where the specimens were collected (Fig. 5), it may be supposed that in the case of *Pleuronectites*, differences in the fluorescence colour are due to increasing alteration of organic compounds during diagenesis. For fossil plant remains, a relationship of fluorescence colour and diagenesis is well known. Although exceptional taxon-specific fluorescence has been described for fossil plants (Wolkenstein & Arp 2021), in general, with increasing thermal maturity during burial, fluorescence intensity of fossil plant remains decreases, accompanied by a shift of the fluorescence emission maximum to the red, finally followed by the extinction of fluorescence (van Gijzel 1967; Teichmüller & Wolf 1977).

Only very few data regarding the thermal maturity of the Muschelkalk in different parts of the Germanic Basin are available. One possibility to assess the thermal maturity of fossils from the relatively organic-poor Middle

Triassic sediments of the Muschelkalk is analysis of the colour of conodonts (Epstein *et al.* 1977). Conodont colour alteration index (CAI) data have been published for the northern Germanic Basin (Nöth 1991) and include sample localities close to those localities where specimens of *Pleuronectites* with colour patterns have been found. Evaluation of these CAI values suggests a correlation of shell fluorescence colour with CAI values. Yellow to orange colour pattern fluorescence is observed for *Pleuronectites* specimens from the northern Harz foreland (Fig. 5, localities 1–5) with corresponding low CAI values of 1 to 1.5, whereas orange-red to no fluorescence is observed for *Pleuronectites* specimens from northern Hesse (Fig. 5, localities 9, 10) with corresponding elevated CAI values of 2.5 to 3.

Most reports of fluorescence in colour patterns of fossil molluscs are about Cenozoic fossils and only very few about Mesozoic fossils (Caze *et al.* 2015). Although preservation of colour patterns is also known from many Palaeozoic molluscs (Kobluk & Mapes 1989), there are no reports of corresponding fluorescence. The lack of reports on fluorescence in colour patterns of Palaeozoic molluscs could therefore be plausibly explained by enhanced diagenetic degeneration of organic compounds by thermal alteration.

CONCLUSION

UV light-induced fluorescence reveals that colour patterns were much more abundant and diverse in basal pectinids than previously thought. Even faint colour patterns of *P. laevigatus* can be traced by fluorescence and true colour patterns can be clearly distinguished from other irregularities in shell colouration. Based on Raman spectroscopy, it can be determined that the colouration of *Pleuronectites* colour bands is due to organic compounds, not to iron oxides. The results show that potential polyene pigments (e.g. carotenoids) or diagenetically altered carotenoids (carotanes) are not preserved and that the fossil pigments consist of aromatic compounds. The following model for the origin and fate of colour pattern fluorescence in *Pleuronectites* can be proposed: (1) diagenetic formation of fluorescent, but colourless breakdown products of the pigments; (2) diagenetic alteration of fluorescent compounds and resulting shift of the fluorescence emission maximum to the red by thermal alteration; (3) diagenetic destruction of fluorescence. It is likely that this model, or parts of it, can also be applied to other fossil shells. Based on the results of the present study, it has to be considered that the fluorescence colour of fossil molluscs may be affected by diagenesis. Therefore, fluorescence colours should only be used with caution for taxonomic purposes, especially if Mesozoic shells or specimens from different localities are studied. On the other side, the results show that by using UV light-induced fluorescence, colour pattern remains can be commonly detected even in marine shells of Triassic age. Further application of this methodology to Mesozoic shells thus has the potential to enhance our understanding of the diversity and evolution of molluscan shell colour patterns.

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (https://doi.org/10.1111/pala.12625):

Appendix S1. List of *Pleuronectites laevigatus* specimens with specific colour patterns (including specimens with uniform colouration).

Figure S1. Influence of sediment matrix on the colour of colour patterns in *Pleuronectites laevigatus* (observed in normal light).

Figure S2. Raman spectra of *Pleuronectites laevigatus*.

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