



Middle Cambrian Bradoriida (Arthropoda) from the Franconian Forest, Germany, with a review of the bradoriids described from West Gondwana and a revision of material from Baltica

Michael Streng¹ · Gerd Geyer²

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Abstract

Bradoriid arthropods (class Bradoriida) are described for the first time from the lower–middle Cambrian boundary interval (regional Agdzian Stage) of the Franconian Forest in eastern Bavaria, Germany. The specimens originate from the Tannenknock and Triebenreuth formations, which are part of a shallow marine succession deposited at the margin of West Gondwana. Five different forms have been distinguished, *Indiana* aff. *dermatoides* (Walcott), *Indiana* sp., *Indota?* sp., *Pseudobeyrichona monile* sp. nov., and an undetermined svealutid, all of which belong to families that have previously been reported from and are typical of West Gondwana. However, at the generic level, all taxa are new for the region. *Indiana* is typical of shallow marine environments. So far it has been reported from Laurentia, Avalonia, and Baltica, and is considered to characterize the paleogeographic vicinity of Cambrian continents. *Pseudobeyrichona* has previously only been recorded from South China, and its new occurrence corroborates previous documentation of taxa from South China in northern West Gondwana. The presence of *Indiana* as a typical “western” taxon and *Pseudobeyrichona* among other typical “eastern taxa” confirms the unique biogeographical position of West Gondwana. The poorly known *Indiana anderssoni* (Wiman) and *Indiana minima* Wiman from the late early Cambrian of Scandinavia have been restudied in order to re-evaluate the two species and to refine the definition of *Indiana*. *Indiana anderssoni* represents a distinct species of *Indiana*, whereas *I. minima* is a pseudo-fossil.

Keywords Cambrian · West Gondwana · Baltica · Bradoriida · Franconian Forest · *Indiana* · *Pseudobeyrichona*

Introduction

The Cambrian of the Franconian Forest area (German: Frankenwald) in north-eastern Bavaria (southern Germany; Fig. 1) has long been known from only a few moderately diverse middle Cambrian trilobite assemblages (e.g., Wurm

1925a, 1928; Sdzuy 1964, 1966, 2000). Recent investigations emphasized that not only are the trilobite assemblages distinctly more diverse than previously assumed (Geyer 2017), but also that the faunas from the Cambrian of the Franconian Forest are surprisingly diverse; they include not only trilobites, articulate brachiopods, hyoliths, and undetermined echinoderm remains (Wurm 1924a, b, 1925a, b; Geyer 2018), but also helcionelloid and pelagiellid molluscs as well as stenotheccoids (Geyer et al. 2018), inarticulate brachiopods, carpod echinoderms (Rahman et al. 2010), graptolites, cancelloriids, hyolithellids, poriferids, and diverse trace fossils (Geyer and Wiefel 1997; Landing et al. 2015; Geyer, unpublished data).

This study presents the first discovered representatives of the Bradoriida, a group of small bivalved basal euarthropods (e.g., Hou et al. 2010), from Cambrian strata of the Franconian Forest area. Bradoriids are extremely uncommon fossils in this area. Despite their rarity, bradoriids show surprising diversity (at least four taxa) in this region, although only

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✉ Michael Streng
michael.streng@geo.uu.se

Gerd Geyer
gerd.geyer@uni-wuerzburg.de

¹ Paleobiologi, Institutionen för geovetenskap, Uppsala universitet, Villavägen 16, 75236 Uppsala, Sweden

² Lehrstuhl für Geodynamik und Geomaterialforschung, Institut für Geographie und Geologie, Bayerische Julius-Maximilians-Universität Würzburg, Am Hubland, 97074 Würzburg, Germany

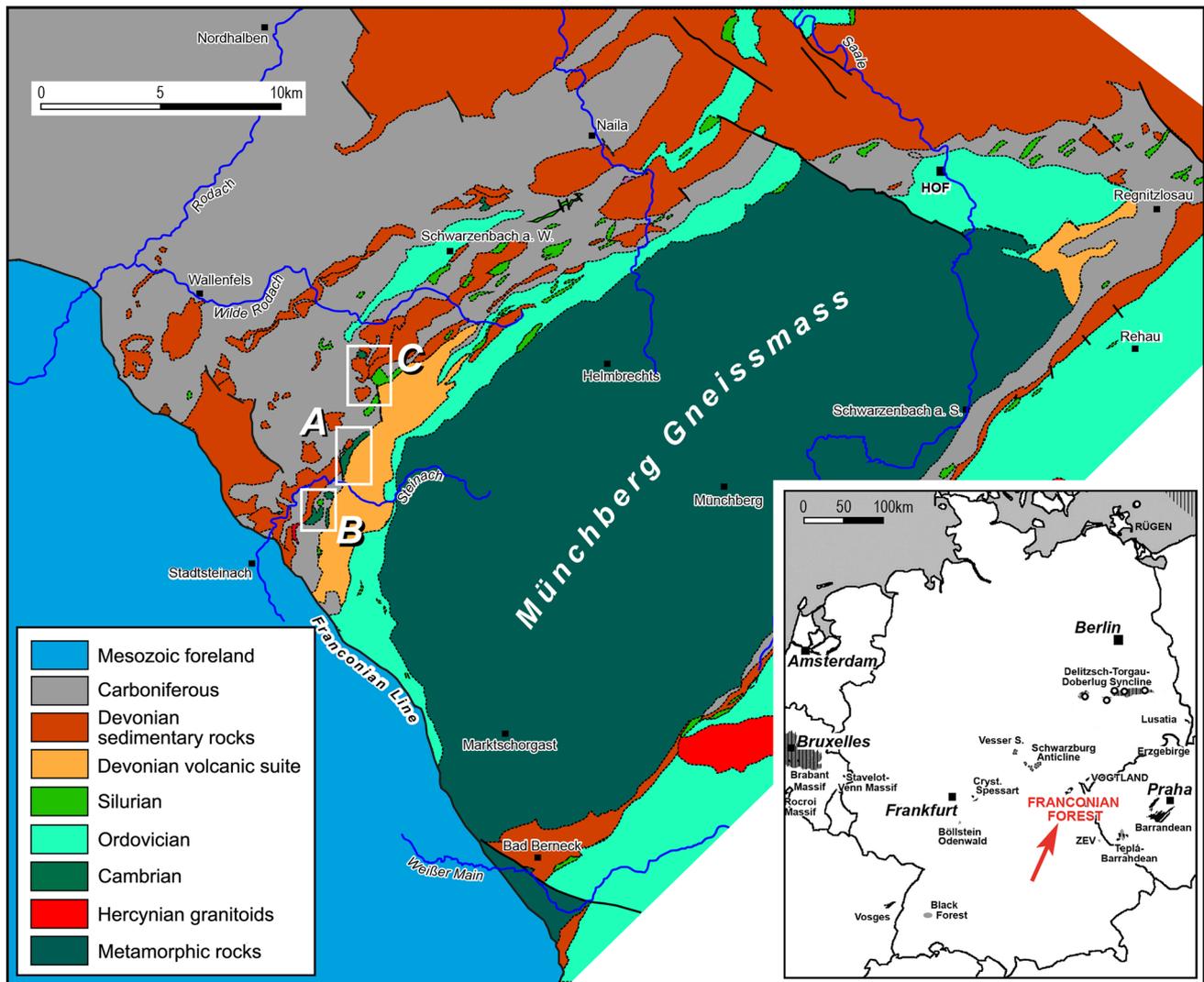


Fig. 1 Generalized geological map of the Saxothuringian Zone in northeastern Bavaria, southern Germany; *small-scale inset map* shows the modern political boundaries of Germany and adjacent regions along with outcrop areas of Cambrian rocks (*black*), outcrop

areas of rocks with supposed Cambrian portions (*gray*), and subsurface Cambrian rocks (*hatched*). *Small white rectangular outlines* refer to areas where tectonic units with Cambrian strata have been found: *A* Wildenstein slice, *B* Triebenreuth slice, *C* Schnebes–Wüstuben slice

one or two specimens of each species or form have been found to date.

Geological setting and stratigraphy

The Franconian Forest lies on the western margin of the Saxothuringian Zone of the Variscan fold belt in north-eastern Bavaria, southern Germany (Fig. 1). This tectonic unit is a West Gondwana-associated terrane or, more accurately, a marginal West Gondwana succession. The Cambrian rocks are interpreted as giant olistoliths in wildflysch of the Variscan orogen (e.g., Linnemann and Schauer 1999), and show a geographically coherent facies succession (Figs. 1, 2).

The “traditional” middle Cambrian succession in the Franconian Forest is dominated by shallow marine fossiliferous units. Unfortunately, the recent choice and ratification of the Cambrian Series 2–Miaolingian and Stage 4–Wuliuan boundary GSSP (IUGS E-Bulletin#144, July 2018) at a very high/young position moves *Paradoxides*-bearing strata in West Gondwana (including the Franconian Forest region) into the revised “early” Cambrian, with the exact position of the boundary unrecognizable to date in West Gondwana. The formations of “traditional” early middle Cambrian age from which the bradoriids were collected are of typical West Gondwanan aspect, similar to those described from the Moroccan Atlas ranges (Geyer and Landing 1995, 2006; Geyer et al. 1995).

Fig. 2 Stratigraphical table of the fossiliferous strata in the Franconian Forest and correlation with global chronostratigraphical units and the standard Cambrian of West Gondwana (Geyer and Landing 2004). Horizons with bradoriids from the Galgenberg Member, the Wildenstein Member, and the lower part of the Triebenreuth Formation are indicated by gray bradoriid outline symbols

GLOBAL CHRONOSTRATIGRAPHY		WEST GONDWANA		FRANCONIAN FOREST	
MIAOLINGIAN Series	GUZHANGIAN Stage	MIDDLE CAMBRIAN	CELTIBERIAN	LANGUE-DOCIAN	Bergleshof Formation ?
	DRUMIAN Stage			CAESAR-AUGUSTAN	Lippertsgrün Formation
	WULIUAN Stage			AGDZIAN	Triebenreuth Formation
(unnamed Series 2)	(unnamed Stage 4)	LOWER CAMBRIAN	ATLASIAN	Wildenstein Member	Tiefenbach Formation ?
				Tannenknock Fm.	Galgenberg Member
	(unnamed Stage 3)			BANIAN	Rauschbach beds ?
				ISSENDALENIAN	

Tannenknock Formation

This formation was traditionally divided into a lower Galgenberg and an upper Wildenstein unit, previously dealt with as formations (Sdzuy 1964; Geyer and Wiefel 1997; Landing et al. 2015), but now regarded as members of the Tannenknock Formation (Geyer 2017). The typical fossiliferous rocks of the Galgenberg Member are light-colored sandy, slightly calcareous blue-gray shales which tend to weather with whitish outer surfaces, whereas Wildenstein fossils are found in fine- to medium-grained, slightly calcareous, commonly feldspathic sandstones or in ocher-weathering sandy calcareous concretions (Geyer et al. 2008; Geyer 2010, 2017). The Galgenberg Member is almost entirely limited to the regional *Kingaspidoides frankenwaldensis* Biozone. The Wildenstein Member belongs to the *Ornamentaspis frequens* Biozone of the Agdzian Regional Stage (Fig. 2).

The Tannenknock Formation is traditionally known from just two isolated olistoliths, termed the Wildenstein (prefix “W” in the locality IDs; within area “A” in Fig. 1) and Triebenreuth (within area “B” in Fig. 1) slices. The vast majority of the specimens dealt with herein come from the Wildenstein slice. The geology of this Wildenstein slice has

been studied in detail by Ludwig (1969) and was remapped and characterized in Geyer (2017, fig. 4).

Triebenreuth Formation

A single specimen, a potential svealutid bradoriid, was collected from rocks of the Triebenreuth Formation (von Gaertner et al. 1968; Ludwig 1969; Geyer and Wiefel 1997; Landing et al. 2015). This formation was first recognized from loose boulders of fossil-bearing calcareous shales found along a forest road on the NW slope of a low hill called Kleiner Torkel, southwest of the village of Triebenreuth in the tectonic Triebenreuth slice (see Landing et al. 2015, fig. 2). The trilobites from this assemblage were recognized by K. Sdzuy to indicate a previously unknown stratigraphical level of middle middle Cambrian age (now Drumian). Despite several attempts to locate the stratigraphical position of the calcareous horizon in the poorly exposed succession, no further fossils have been found (von Gaertner et al. 1968; Ludwig 1969).

Ludwig (1969) described volcanic rocks from an adjacent locality as both quartz porphyrites and spilitic rocks, and assigned these volcanic rocks to the same stratigraphic unit as the mudstones. He regarded the volcanic horizons

as the base of this (unnamed) new formation. Landing et al. (2015) were able to date a volcanic tuff from these horizons, providing the first precise and biostratigraphically bracketed date within the traditional middle Cambrian of central Europe. This tuff had a weighted mean ^{206}Pb – ^{238}U date of $503.14 \pm 0.13/0.25/0.59$ Ma based on zircons, as determined by U–Pb chemical abrasion isotope dilution mass spectrometry (CA-TIMS) techniques.

A second locality assigned to the Triebenreuth Formation was reported by Junker (1971) and Sdzuy (1972), who assigned an unillustrated fauna to the “*Paradoxides oelandicus* Stage,” which would make it distinctly older than the fauna from the Kleiner Torkel. The subsequently published explanatory notes for the relevant map sheet, 1:25,000 Schwarzenbach am Wald, described strata of the Triebenreuth Formation supposedly from this locality near Wustuben. The base of the formation is purportedly diabase breccias and keratophyre breccias with a mudstone matrix (von Horstig and Stettner 1976). Subsequent investigations by GG did not confirm these data. However, a surprisingly diverse fauna was recently collected by Stefan Meier (Marktredwitz) from nearby rocks, consisting of calcareous nodules in a volcanoclastic matrix from fields near Wustuben (ca. 4.3 km NNE of the northern tip of the Wildenstein slice (ca. N50°15'0", E11°34'20")). These rocks appear to cover at least two trilobite biozones, the upper one with *Badulesia tenera*, indicating that the rocks range into the Drumian but are older than the dated volcanic breccia of the Kleiner Torkel. The potential svealutid carapace comes from this newly investigated locality near Wustuben in the Schnebes–Wustuben slice.

Age and correlation

Despite the extremely limited sample size, the trilobite faunas from the Tannenknock and Triebenreuth formations are comparatively diverse and enable a precise correlation with other Cambrian areas of West Gondwana (Fig. 2). They are particularly similar to the trilobite faunas from the Jbel Wawrmast Formation of the Moroccan Atlas ranges. *Kingaspidoidea frankenwaldensis* (Wurm, 1925b), a species that is characteristic for the Galgenberg Member of the Tannenknock Formation, has been found in the *Moroccocus notabilis* Biozone (earlier the *Cephalopyge notabilis* Biozone) of the eastern Anti-Atlas (Geyer and Vincent 2014). The trilobite association of the Wildenstein Member is characterized by *Ornamentaspis frequens* Geyer, 1990a, a species that is an index fossil for the *O. frequens* Biozone in the Moroccan Atlas ranges. This zone directly overlies the *M. notabilis* Biozone (Geyer 1990b), thus providing a perfect match for the formations in the Franconian Forest (Geyer et al., in press).

The rocks of the Triebenreuth Formation from near Wustuben belong to a succession that is superficially similar to the Wildenstein Member of the Tannenknock Formation, but with a considerable content of volcanoclastic material. The trilobite fauna, as yet unpublished, indicates previously unknown younger strata of late Agdzian–early Caesaraugustan regional stages (Fig. 2). At least two biozones appear to be represented in the loose blocks from which the material was collected, the younger one coinciding with the well-known *Badulesia tenera* Biozone recognized from regions such as the Iberian Peninsula, the Moroccan Atlas ranges, and western Avalonia.

Localities and collections

Due to the extremely small outcrop areas, in combination with dense forested vegetation or agricultural use, the collection of Cambrian fossils in the Franconian Forest area is arduous, or depends on fortunate temporary exposures. The fossils described herein are derived from the Galgenberg and Wildenstein members of the Tannenknock Formation (Cambrian Stage 4/Wuliuan boundary interval) originating from the Wildenstein slice (Fig. 1a), except for a single specimen from the Triebenreuth Formation of the Schnebes–Wustuben slice (Fig. 1c). Sampling levels are shown in Fig. 2 and locations are provided in the Appendix. The samples originate from unstudied collections of K. Sdzuy (mostly from 1956), GG (1979–2013), and recent collections by Stefan Meier (Marktredwitz).

Preservation

The sandy shales of the Galgenberg Member yield shelly fossils in which the shell/carapace is preserved in various modes of pseudomorphy. In the bradoriids, the original shell material is now altered into ferric material, but with a phosphatized internal mold. Unfortunately, phosphatization did not just replace the shell; growth obviously persisted, meaning that fine details of the exterior are not well preserved (Fig. 3a).

Similar preservation occurs in the specimens from the Wildenstein Member at sample locality W8. The rocks from this location represent large carbonate nodules with a more or less strong secondary calcification of siliciclastic material, in which bradoriids and other fossils may be preserved with a phosphatic plug or internal mold. Other fossils indicate selective phosphatization. Phosphatization took place early in the diagenetic process because details of the internal shell surface are preserved with fidelity prior to the dissolution of the shell or carapace (e.g., Vendrasco et al. 2010). The phosphatic partial steinkerns of the Wildenstein

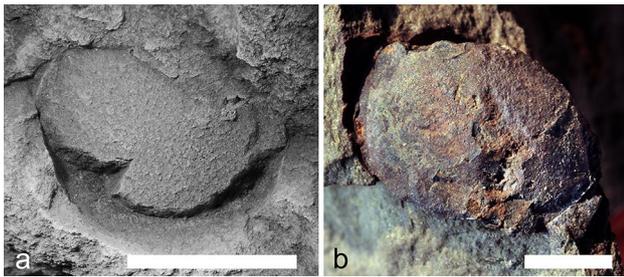


Fig. 3 Examples of bradoriid preservation. **a** *Indiana* sp., MMUW 2018A-001, incomplete carapace with partial internal phosphatic mold; Tannenknock Formation, Galgenberg Member, sample locality W12; lateral view of left valve. **b** *Indiana* aff. *dermatoides* (Walcott, 1887), SSMM 12010, incomplete carapace preserved as internal mold with parts of the carapace included in the phosphatized plug; Tannenknock Formation, Wildenstein Member, sample locality W8; left lateral view. Scale bars 3 mm

bradoriids (and hyoliths) are incomplete. In other examples, the carapace is partially preserved and forms a unit together with the phosphatic internal plug (Fig. 3b).

Bradoriids of West Gondwana

Bradoriids are rare in Cambrian rocks of West Gondwana, most probably owing to a dominance of shallow to extremely shallow marine shelf facies with a prevalence of siliciclastic deposits in the successions. Nevertheless, about 20 taxa of bradoriids have been described from lower and middle Cambrian strata from the Moroccan Atlas ranges, the Iberian Peninsula, south-western Sardinia, Normandy and the Montagne Noir in France, the Torgau–Doberlug Synclinorium in Saxony, Germany, the Barrandian of the Czech Republic, and the Dead Sea region of Jordan.

The reports from Morocco include the Bradoriidae *Bradoria mapora* Hinz-Schallreuter, 1993 and *Ifersiktia mipora* Hinz-Schallreuter, 1993 from Jbel Azgza and Jbel bou Ifersikht, respectively, in the central Anti-Atlas (both probably from the *Ornamentaspis frequens* Biozone); the putative beyrichonid *Tagra koppkai* Hinz-Schallreuter, 1993 from the *Ornamentaspis frequens* Biozone of the Tagragra Syncline, central Anti-Atlas; the hipponicharionids *Hipponicharion geyeri* Hinz-Schallreuter, 1993 (probably from the *Ornamentaspis frequens* Biozone of Tizi n'Zem in the eastern Anti-Atlas) and *Hipponicharion taidaltensis* Gozalo and Hinz-Schallreuter, 2002 (from the *Sectigena* Biozone, lower Cambrian Stage 4, of the Taïdalt section, western Anti-Atlas); and *Albrunnicola oelandicus maroccanus* Hinz-Schallreuter, 1993 from the *Bailiella* cf. *levyi* Biozone, Guzhangian, of Ait Mersid, central Anti-Atlas, representing the youngest known bradoriid from West Gondwana. *Bradoria mapora*, *Ifersiktia mipora*, *Tagra koppkai*, and

Hipponicharion geyeri all occur at a stratigraphical level more or less equal to that of the Wildenstein Member of the Tannenknock Formation, from which *Indiana* aff. *dermatoides*, *Indota?* sp., and *Pseudobeyrichona monile* sp. nov. are described herein. However, the Bavarian species are distinct from the species described from the Anti-Atlas. This is remarkable because of the relatively close resemblance of trilobites and mollusks of the Tannenknock Formation to those from coeval strata of the Jbel Wawrmast Formation of southern Morocco.

Bradoriid taxa from the Iberian Peninsula include one of the oldest forms known from West Gondwana, i.e., the cambriid *Cordubiella pedrochensis* Hinz-Schallreuter, Gozalo and Liñan, 2008 from the “Ovetian” (*Lemdadella* Biozone, late Issendalenian) of southern Spain. Younger Iberian taxa are represented by three hipponicharionids, i.e., *Hipponicharion hispanicum* Gozalo and Hinz-Schallreuter, 2002 from the lower Cambrian (“Marianian” = Banian) Alconera Formation of the Sierra Nevada, southern Spain, and two taxa described by Gozalo et al. (2004) from the western Iberian Chains of northern Spain as *Hipponicharion* aff. *hispanicum* from the Daroca Formation (*Hupeolenus* Biozone) and *Wimanicharion* aff. *matthewi* (Wiman 1903) from the Valdemiedes Formation. The age of the latter taxon is comparable to the *Ornamentaspis frequens* Biozone and hence roughly coeval to the taxa from the Franconian Forest.

Specimens described as *Indianites caenensis* Cobbold, 1935 were the first bradoriids reported from France, and also represent the oldest species currently known from West Gondwana. This poorly known taxon, which might in fact be a simple svealutid (see the “Discussion” of *Indiana* below), is from the Saint-Jean-de-la-Rivière Formation near Carteret, Normandy (e.g., Doré 1994), where it co-occurs with *Bigotina bivallata* Cobbold, 1935, indicating an early “Ovetian” (= early Issendalenian) age (*Bigotina* Biozone; see e.g., Gozalo et al. 2003, Zhang et al. 2017, Geyer, in press). Vannier and Williams (in Vannier et al. 2005) described three cambriid taxa from shales of the lower Cambrian Pardailhan Formation from the Montagne Noir in southern France: *Monceretia erisylvia* Vannier and Williams, 2005, *Cambria danvizcainia* Vannier and Williams, 2005 and *Matthoria?* sp. Putative juvenile specimens of *M. erisylvia* and *Matthoria?* sp. were subsequently reported and illustrated by Devaere et al. (2014) from limestone horizons of the same formation.

A single bradoriid species, *Hipponicharion ichnusum* Elicki and Pillola, 2004 (= *Hipponicharion eos* Matthew, 1886 according to Dies Álvarez et al. 2008), was described from the uppermost lower Cambrian Campo Pisano Formation of southwestern Sardinia. *Hipponicharion elickii* Gozalo and Hinz-Schallreuter, 2002, another representative of the widespread genus *Hipponicharion*, is the only reported bradoriid from the Torgau–Doberlug Synclinorium

of Saxony (Cambrian Zwethau Formation, Cambrian Stage 3; Elicki 1994, 2007).

Příbyl and Vaněk (1965) described *Hipponicharion snajdri* Příbyl and Vaněk, 1965 from the middle Cambrian Jince Formation of the Czech Republic and illustrated a potential second species as *Hipponicharion* aff. *snajdri* Příbyl and Vaněk, 1965. Šnajdr (1975) revised the taxa on the basis of new material and considered both forms to represent distinct species of the new hipponicharionid genus *Konicekion*, i.e., *K. snajdri* (Příbyl and Vaněk, 1965) and *K. radion* Šnajdr, 1975. In addition, a third species of *Konicekion*, *K. tix* Šnajdr, 1975, was introduced, representing the type and youngest species of the new genus. However, considering the morphological variability observed in other bradoriid species linked to ontogeny, preservation, and/or potentially environmental factors (e.g., Siveter and Williams 1997; Hou et al. 2002; Zhang 2007), it is likely that the three species of *Konicekion* represent merely a single species. Likewise, Fatka et al. (2014) considered the status of the three species as uncertain and in need of re-evaluation. Potential synonymy of *Konicekion* with *Albrunnicola* Martinsson, 1979 was suggested by Hinz-Schallreuter (2006). Fatka et al. (2014) also described two additional taxa from the Jince Formation tentatively assigned to the kunmingellid *Emeiella* Li, 1975 as *Emeiella* sp. and to the svealutid *Liangshanella* Huo, 1956 as *Liangshanella* aff. *liangshanensis* Huo, 1956. A third taxon was illustrated as *Liangshanella* sp. (Fatka et al. 2014, fig. 2g).

An unnamed bradoriid from the Numayri Member of the Burj Formation (*Kingaspis campbelli* Biozone) from the Wadi Zarqa Ma'in section, Dead Sea, Jordan (Elicki 2011), more or less coeval with part of the Tannenknock Formation, resembles *Indiana* in outline, but differences in size, lack of distinct characters, and unsatisfactory preservation make comparison conjectural.

Biogeographic relationships

As outlined above, the early Cambrian bradoriid record of West Gondwana (Issendalenian and Banian regional stages) is characterized by the Family Cambriidae Li, 1975 recognized in France and Spain (Vannier et al. 2005; Hinz-Schallreuter et al. 2008) and the genus *Hipponicharion* with occurrences in Morocco, Spain, and Germany (Gozalo and Hinz-Schallreuter 2002). A potential svealutid indicates that the Family Svealutidae Öpik, 1968 might also be present in West Gondwana early on. In contrast, Middle Cambrian (Agdzian, Caesaraugustian, and Languedocian regional stages) deposits reveal a diversity of hipponicharionid taxa in Morocco, Spain, and the Czech Republic, and representatives of the Family Bradoriidae Matthew, 1902 in Morocco (Šnajdr 1975; Hinz-Schallreuter 1993; Gozalo et al. 2004).

The recently reported svealutid and kunmingellid specimens from the Czech Republic (Fatka et al. 2014) increase the middle Cambrian diversity in West Gondwana, a diversity that is further corroborated by the five middle Cambrian taxa from the Franconian Forest described below. They belong to the families Bradoriidae, Hipponicharionidae Sylvester Bradley, 1961, and Svealutidae. Biogeography based on bradoriids is intricate. Increasing data on the spatial and stratigraphical distribution of the Bradoriida, as well as the ecology and potential facies dependency of the individual taxa, have weakened previously established biogeographic patterns (see review by Williams et al. 2007). This is also demonstrated by the taxa from the Franconian Forest. All of the five distinguished forms, i.e., *Indiana* aff. *dermatoides* (Walcott, 1887), *Indiana* sp., *Indota?* sp., *Pseudobeyrichona monile* sp. nov., and an undetermined svealutid, appear to be new for West Gondwana. *Indiana* Matthew, 1902 has previously been reported from lower and lower middle Cambrian rocks in Laurentia (e.g., Ulrich and Bassler 1931a, Siveter and Williams 1997), Avalonia (e.g., Williams and Siveter 1998), and Baltica (e.g., Wiman 1903), and was considered to be characteristic of the so-called Olenellid Province (sensu McKerrow et al. 1992) by Williams et al. (2007), but the concept of such a trilobite faunal province is now redundant because it was based on the idea of a close phylogenetic relationship of olenellids and holmiids. Nevertheless, *Indiana* reconfirms the assumptions of a clustered distribution of these Cambrian continents and thus contributes to paleogeographic reconstructions. *Pseudobeyrichona* Shu, 1990a is so far only known from the lower Cambrian (Cambrian Series 2, Stage 3) of the South China continent, but its occurrence parallels other reports of typical Chinese taxa in West Gondwana, i.e., *Emeiella* sp. in the middle Cambrian of Perunica (Fatka et al. 2014). The occurrence of *Indiana* and taxa typical for South China in West Gondwana seems to confirm the unique biogeographic position of this area as being intermediate between the purported “Olenellid” and “Redlichiid Trilobite Provinces” (e.g., Cowie 1971, Pillola 1990), or between the western and eastern bradoriid faunal provinces of Huo and Shu (1985). However, it is more striking that the new reports from the Franconian Forest region reconfirm the similarity of faunas between Baltica, West Gondwana, and Avalonia, which can be regarded as a “Holmiid Province.”

Systematic paleontology

Remarks. The description of the bradoriid taxa generally follows the terminology used by Siveter and Williams (1997) and Williams and Siveter (1998), but see also Zhang (2007) and Peel and Streng (2015). Specimens from the Franconian Forest are deposited in the collection of the

Mineralogical Museum of the Würzburg University (acronym MMUW) and the Stefan Meier collection, Marktredwitz (acronym SSMM). Material studied for comparison, i.e., specimens of *Indiana anderssoni* (Wiman, 1903) and *Indiana minima* Wiman, 1903, are housed in the paleontological collections of the Museum of Evolution, Uppsala University (acronym PMU).

Order **Bradoriida** Raymond, 1935

Family **Bradoriidae** Matthew, 1902

Diagnosis (modified after Williams and Siveter 1998, p. 11 and Streng et al. 2008, p. 14). Medium to large sized (adults up to 14 mm in length), subamplete to strongly postplete Bradoriida with subequivalved carapace without posterior gape. Dorsum typically straight; hinge-line well developed, shorter than carapace length. Commissure straight. Anterodorsal node developed or absent. In addition, a prominent node in the median to mid anterior or dorsomedian position might be developed. If present, marginal structure is a very narrow ridge. Comarginal furrow or concave zone might be developed, situated some distance from the free margin, often separating a more flattened marginal area from convex central area of carapace. Valves have concentric striation or reticulostriation, punctation, or are smooth.

Genera included. *Bradoria* Matthew, 1899 (= *Bradorona* Matthew, 1902; ?= *Ifersiktia* Hinz-Schallreuter, 1993); *Walcottella* Ulrich and Bassler, 1931a; *Indiana* Matthew, 1902 (= *Indianites* Ulrich and Bassler, 1931b); *Indota* Öpik, 1968 (?= *Tropidiana* Öpik, 1968) (see Siveter and Williams 1997 and Streng et al. 2008).

Discussion. Streng et al. (2008) modified the family diagnosis provided by Williams and Siveter (1998) by including the possibility of the development of a flattened area along the free margin of the valves. This was to include a potential new taxon from the lower Cambrian of Sweden described as *Walcottella?* aff. *apicalis*. An equivalent area also appears to be developed in *Indota?* sp. from the middle Cambrian of Germany described below. The diagnosis is herein furthermore specified by adjusting the size range and potential outline of the valves. The family diagnosis of Williams and Siveter (1998, p. 11) (see also Siveter and Williams 1997) erroneously states “Medium sized (adults c. 6–7 mm long), postplete Bradoriida...,” which would exclude typical bradoriid taxa such as *Indiana* and *Walcottella*, which are large (up to 14 mm) and subamplete, respectively (Siveter and Williams 1997).

Genus *Indiana* Matthew, 1902

Type species. *Indiana lippa* Matthew, 1902, p. 463, pl. 2, fig. 10a–d (subsequent designation by Ulrich and Bassler, 1931a, p. 68) from the Dugald Formation (*Eccaparadoxides etemnicus* Biozone, late Wuliuan), Cape Breton Island, Canada.

Diagnosis (modified after Siveter and Williams 1997, p. 29). Medium to large bradoriids (adults up to 10–14 mm long) with elongate postplete carapace; length of carapace is generally one-third greater than its height. Length of hinge-line variable, about 40 to 65% of valve length. Lateral outline of nondorsal parts of valve gently curved but commonly with straight posterodorsal margin. No lobation, nodation, or marginal structures; valves are gently and evenly convex in transverse section. Valves have concentric granulostriation, punctation, or are smooth.

Discussion. Since the introduction of the genus *Indiana* by Matthew (1902), the concept of the genus changed considerably. In his original description, Matthew (1902) considered an evenly rounded, oval to ovate outline with a straight hinge line in combination with a typically present anterocentral node to be characteristic of this new genus. In their emendation of the genus, Ulrich and Bassler (1931a) realized that the hitherto considered type species, *Indiana ovalis* Matthew, 1902, is more likely a species of *Bradoria* and assigned *Indiana lippa* Matthew, 1902 instead as the type species. According to Ulrich and Bassler (1931a), *Indiana* is characterized by the lack of any nodes and a truncated elliptical (postplete) outline with a straight hinge line. The valves are punctate and a delicate rim can be developed along the free margin. Siveter and Williams (1997) and Williams and Siveter (1998) reviewed the Laurentian, Avalonian, and some additional species of the genus and provided a stricter diagnosis regarding shape, proportions, and size. They excluded taxa with distinct marginal structures and comparatively small species from the genus, e.g., *Indiana sipa* Fleming, 1973. Their diagnosis is generally followed herein, with one modification. Siveter and Williams (1997, p. 29) considered a hinge line with a dimension between one-half and two-thirds of the valve length to be diagnostic of *Indiana*, but *I. dermatoides* (Walcott, 1887) has a hinge-line shorter than half of the valve length (Siveter and Williams 1997, p. 33). The diagnosis given above has accordingly been adjusted to also include characters of *I. dermatoides*.

More than 20 species have been described or re-assigned to *Indiana* (e.g., Ulrich and Bassler 1931a; Kempf 1986; Shu 1990a), most of which are considered to be junior synonyms of other species of *Indiana*, to belong to other genera, or to represent poorly preserved indeterminate specimens

(see Siveter and Williams 1997 and Williams and Siveter 1998 for details). Accordingly, Williams and Siveter (1998) deemed only five species to be included in *Indiana*. Among these, *I. lippa*, *I. secunda* (Matthew, 1895), *I. dermatoides* and *I. anderssoni* (Wiman, 1903) are similar in being postplete, evenly convex, and having a relatively straight hinge line that is linked posteriorly to a distinct, straight (or nearly so) posterodorsal margin. The four species differ in the shape of the postplete outline, in the relative lengths of the hinge line and posterodorsal margin, the posterior cardinal angle, and in the carapace ultrastructure being punctate (*I. anderssoni*, *I. dermatoides*, *I. secunda*) or smooth (*I. lippa*). This contrasts with the fifth species, *I. lentiformis* (Cobbold, 1921), which is characterized by an apparently convex dorsal margin, valves with an anteroventral flattened region, the lack of a clearly defined posterodorsal margin, and a valve ornament of granulostriation. *Indiana anderssoni*, described from a Pleistocene glacial erratic boulder of late early Cambrian age collected on the Swedish island of Egggrund (Wiman 1903), is one of the least known species of *Indiana*, and has not been re-studied since its original description; it is re-described herein for comparison with the specimens from the Franconian Forest assigned to *Indiana*. Wiman (1903) also proposed *Indiana minima*, a species subsequently queried as to whether it belongs to *Indiana* due to its small size and convex dorsal margin; however, in the absence of a suitable genus, it has been (questionably) kept within *Indiana* (Ulrich and Bassler 1931a). *Indiana minima* has also been re-investigated and shown not to represent a fossil (see below).

The genus *Indianites* Ulrich and Bassler, 1931b is an objective synonym of *Indiana* Matthew, 1902 (see International Commission on Zoological Nomenclature 1959 for details), and species originally assigned to *Indianites* must be considered species of *Indiana*. However, taxonomic concepts have changed since the description of these species, and their affiliation with *Indiana* should thus be re-assessed individually. After having studied its type material, Siveter and Williams (1997) referred *Indianites tennesseensis* Resser, 1938 to *Indota*, and Williams and Siveter (1998) considered *Indianites exigua* Cobbold in Cobbold and Pocock, 1934 to be a species of *Ovaluta* Zhang, 1987. Other species of *Indianites* still await a re-evaluation. Among these are *Indianites obtusa* Cobbold in Cobbold and Pocock, 1934, *Indianites caenensis* Cobbold, 1935, and *Indianites ovooides* Kautsky, 1945. *Indianites obtusa* from the *Lapworthella* Limestone of Shropshire, England (so-called “*Protolenus* Biozone,” Cambrian Stage 4) has a similar outline to *Indiana*, but with a length of only 1 mm it appears to be too small to be a legitimate species of *Indiana*. The same is also true for *Indianites caenensis* from the *Bigotina bivallata* Biozone (near base of Cambrian Stage 3) of Carteret, Normandy, France (which is regarded as part of the Armorican

microplate collage). A punctate ultrastructure of the valve, as is characteristic of *Indiana*, has been described for this species (Cobbold 1935), but the small size and the presence of a narrow brim suggest reference to the Svealutidae, particularly to genera such as *Ovaluta* or *Liangshanella*. Punctate ultrastructure is also known from the Svealutidae, from which it has been described from the more or less coeval *Ovaluta salopiensis* (Cobbold in Cobbold and Pocock, 1934) from the Comley Sandstone of Shropshire, England (Williams and Siveter 1998). In fact, *O. salopiensis* and *I. caenensis* might be synonymous.

In contrast to *Indianites obtusa* and *I. caenensis*, the size and outline of *Indianites ovooides* from the upper part of Cambrian Stage 4 (revised *Ellipsocephalus linnarssoni* Biozone sensu Nielsen and Schovsbo 2011) of central Lapland, northern Sweden, are characteristic of *Indiana*. The presence of an anterior flattened marginal area as well as its irregular striated surface (“...dünne unregelmässige drahtartige Runzeln...” in Kautsky 1945, p. 149) are reminiscent of *Indiana lentiformis*. According to Kautsky (1945), the hinge line of *I. ovooides* is less than half of the shell length, which would contradict a synonymy with *I. lentiformis*. *Indiana ovooides* (Kautsky, 1945) is here considered a distinct species of *Indiana* that is close to *I. lentiformis*. Unfortunately, the single (holotype) specimen of *I. ovooides* appears to be lost from the collections of the Swedish Museum of Natural History in Stockholm and thus was not available for re-examination.

The genus *Sinskolutella* was erected by Mel’nikova (1998) to accommodate the previously described early Cambrian taxa *Bradoria ordinata* Mel’nikova in Grigor’eva et al., 1983 and *Leperditia? concentrisulcata* Abushik, 1960 from the Siberian Platform (see Mel’nikova et al. 1997; Mel’nikova 1998; Peel et al. 2016 for details). Subsequently, Mel’nikova (2001) questionably added the new species *Sinskolutella? kazimierae* from the lower Cambrian of Poland to the genus. With the accommodation of the type species *Bradoria ordinata* in *Matthoria* Siveter and Williams, 1997 (Williams et al. 2007), *Sinskolutella* became a junior synonym of *Matthoria*. However, “*Sinskolutella*” *concentrisulcata* and “*Sinskolutella?*” *kazimierae* lack the characteristic dorsal cusp of *Matthoria* and are better compared with other genera. “*Sinskolutella*” *concentrisulcata* might be best assigned to *Liangshanella*, whereas “*Sinskolutella?*” *kazimierae* appears to be close to typical species of *Indiana*. Like the species of *Indiana*, “*Sinskolutella?*” *kazimierae* is postplete, has a straight dorsal and posterodorsal margin, a similar size, and a smooth carapace. However, according to Mel’nikova (2001, p. 279), a “narrow flat area [is] developed along the free margin,” contradicting an affinity with *Indiana*. Re-studying the single known carapace might show that the “flat area” in the depicted right valve (Mel’nikova 2001, pl. 8, fig. 7a) is the inner margin of the opposing left valve, i.e., the result of a subequivalved carapace.

Species included. Besides the type species, five additional species are herein included in *Indiana*, i.e., *I. dermatoides* (Walcott, 1887), *I. secunda* (Matthew, 1895), *I. anderssoni* (Wiman, 1903), *I. lentiformis* (Cobbold, 1921), and *I. ovoides* (Kautsky, 1945) (see also the “Discussion” above).

Occurrence. Lower and middle Cambrian (Cambrian Stages 3 to 5) of Avalonia, Baltica, eastern Laurentia (New York State, East Greenland) (see Kautsky 1945, Williams and Siveter 1998; Streng et al. 2008; Skovsted 2006; and Williams et al. 2007 for details) and West Gondwana (Germany) (herein).

Indiana* aff. *dermatoides (Walcott, 1887)

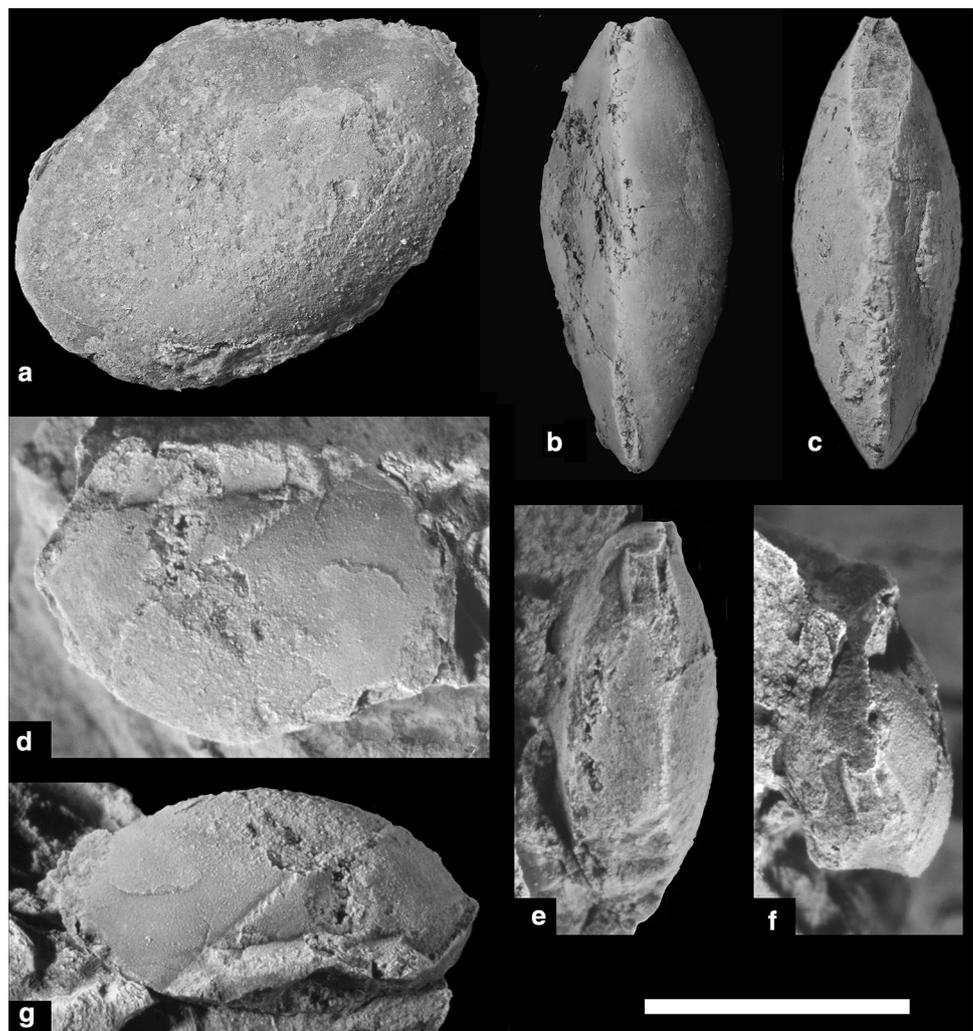
Figures 3b, 4a–c

Material. Phosphatic composite molds of two carapaces: MMUW 2018A-003, small specimen with incomplete anterodorsal margin (Fig. 4a–c), from the Wildenstein Member of the Tannenknock Formation, sample horizon

W13b, Wildenstein slice; SSMM 12010, larger specimen with incomplete posteroventral margin (Fig. 3b), from the Wildenstein Member of the Tannenknock Formation, sample horizon W8, Wildenstein slice.

Description. Specimens are equivalved, distinctly postplete in shape, measuring 3.3 mm and 8.5 mm in length, 2.7 mm and 6.6 mm in height; the small specimen is 1.4 mm wide. Dorsal margin straight with well-developed hinge line, ca. 1.6 mm and 4 mm long, respectively, constituting 47–48% of carapace length. Free margin mostly evenly rounded with posterodorsal and anterodorsal curves indistinct, but with long straight posterodorsal margin, which encloses an obtuse angle with dorsal margin, measuring ca. 139° in the small specimen and ca. 142° in the large specimen. Anterior cardinal angle also obtuse but less than in posterior one, measuring ca. 123° in the small specimen and 117° in the large specimen. Anterodorsal margin poorly preserved in the small specimen and relatively long and straight in the larger one. Posterodorsal and dorsal margin about equal in length.

Fig. 4 Specimens from the Tannenknock Formation referred to *Indiana* Matthew, 1902. **a–c** *Indiana* aff. *dermatoides* (Walcott, 1887), MMUW 2018A-003, carapace, sample locality W13b, Wildenstein Member: **a** lateral view of right valve; **b** dorsal view (anterior pointing up); **c** ventral view showing partially missing antero- to anteroventral margin (anterior pointing up). **d–g** *Indiana* sp., SSMM 10267, deformed incomplete carapace of *Indiana* sp., sample locality W2, Galgenberg Member: **d** lateral view of presumed left valve; **e** oblique dorsal view showing deformed hinge area; **f** oblique posterior view with posteroventral margin missing; **g** anterior view showing preservation of anterior and anterodorsal margin. Scale bar equals 2 mm for **a–c** and 5 mm for **d–f**



Points of maximum length on posterior and anterior margin at different positions in relation to height, with posterior one situated relatively low at 35–38% of the height, whereas anterior one is at about 75% of the height in the small specimen (exact position uncertain because of the incompletely preserved anterior margin), and at about 60% of the height in the large specimen. In transverse section, valves are evenly convex without any lobation. Exterior surface of molds corroded, showing various levels of preservation of the original carapace. Smooth areas as well as areas ornamented with minute knobs and pores (ca. 60 µm in diameter) have been observed.

Discussion. The relative short hinge line, as well as the other characters of the described specimens, generally agree with the description of *I. dermatoides* by Siveter and Williams (1997) from the late early Cambrian of eastern Laurentia (New York State). However, typical specimens of *I. dermatoides* are markedly postplete, a feature that is less distinct in the specimens from Bavaria. The small specimen (length 3.3 mm) is smaller than typical specimens of the species, where specimens illustrated by Siveter and Williams (1997, pl. 4, figs. 6–8) reach 5.3 to 5.6 mm in length. Hence, it might represent a juvenile in which the strongly postplete carapace outline is not yet fully developed. The large specimen is larger than the types illustrated by Siveter and Williams (1997), but its precise outline is uncertain on account of the broken posteroventral margin. Nevertheless, judging from the size of the missing edge of the mold, it seems unlikely that the specimen was originally markedly postplete. Considering the differences in outline between the Bavarian specimens and *I. dermatoides*, in combination with their distinct geographic and stratigraphical separation, it seems more likely that the specimens from Bavaria represent a new species of *Indiana*. Given the poor preservation, no new species is formally erected. *I. aff. dermatoides* differs from the time-equivalent *I. lippa* from the middle Cambrian (Acadian Series) of western Avalonia (Nova Scotia and New Brunswick, see Siveter and Williams 1997) in having a shorter hinge line. The locally observed knobs and pores on the preserved outer surface of *I. aff. dermatoides* are interpreted as remnants of the punctate ultrastructure that is characteristic of *I. dermatoides* and other species of *Indiana* (Walcott, 1887; Ulrich and Bassler, 1931a; Siveter and Williams, 1997).

Occurrence. *Ornamentaspis frequens* Biozone, Agdzian Regional Stage (lower middle Cambrian) of West Gondwana, probably coeval with lowermost Wuliuan Global Stage; Wildenstein Slice, Franconian Forest, northeastern Bavaria, Germany.

Indiana sp.

Figures 3a, 4d–g

Material. Two specimens from the Galgenberg Member of the Tannenknock Formation: one incomplete internal mold of a fractured carapace (Fig. 4d–g), SSMM 10267, sample horizon W2, Wildenstein slice; one mold of an incomplete left valve (Fig. 3a), MMUW 2018A-001, sample horizon W12, Wildenstein slice; both specimens with major parts of the free margin missing.

Description. Preserved mold of the carapace measures 8.1 mm in length and 5.8 mm in height. Dorsal margin straight with well-developed hinge line, ca. 4.4 mm in length, which encloses an angle of ca. 125° with a straight anterodorsal margin and of ca. 145° with preserved parts of the posterodorsal margin. Free margin incomplete, with only partly preserved antero- and posterodorsal margins; exact outline of carapace is thus unknown. Surface of carapace without lobation, smooth, but locally with small pustules preserved. The incomplete left valve measures 3.9 mm in length and has a straight dorsal margin of at least 2.4 mm. Anterodorsal margin partly preserved, enclosing an angle of ca. 122° with dorsal margin. Posterodorsal margin not clearly seen as distinguishing between the specimen and the host rock is difficult. Preserved surface of mold with a grainy texture.

Discussion. Despite the incomplete preservation of the two specimens, all observed characters indicate an affiliation with *Indiana*. These characters include the size of the valves, the lack of any lobation, and the angles enclosed by the antero- and posterodorsal margins with the hinge line, which are similar to angles observed in species of *Indiana* (e.g., Siveter and Williams 1997). In addition, locally preserved pustules in one of the specimens are reminiscent of those seen in *Indiana aff. dermatoides*, suggesting an originally punctate carapace. Orientation of the specimens is based on the measured cardinal angles, which suggest that the smaller angle is anterior, analogous to angles observed in species of *Indiana* or *Bradoria*. The affiliation with *Indiana* would require a postplete outline, which is not evident in either of the specimens due to the incomplete preservation of the ventral free margin. As the specimens are from the same formation as *I. aff. dermatoides*, it is likely that they belong to the same taxon. However, due to the incompleteness of the free margin and the general poor preservation of the specimens, the specimens have been left in open nomenclature.

Occurrence. *Kingaspidoides frankenwaldensis* Biozone, Agdzian Regional Stage, probably coeval with the late part of the Cambrian Stage 4; Franconian Forest (northeastern Bavaria, Germany). West Gondwana.

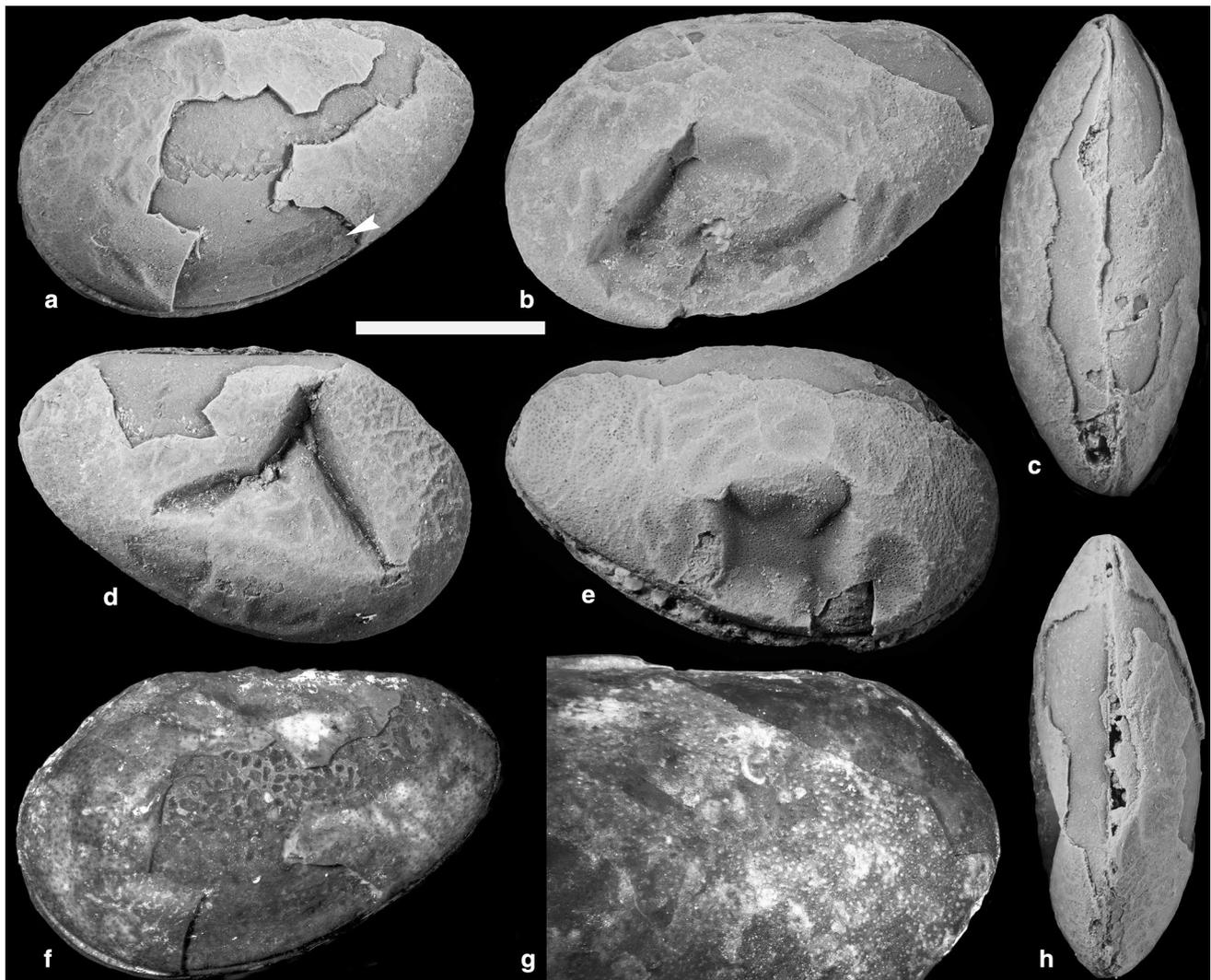


Fig. 5 *Indiana anderssoni* (Wiman, 1903) from an erratic boulder found on Eggegrund Island, Sweden. **a, d, f, h** PMU22583, lectotype (specimen illustrated by Wiman 1903, pl. 1, figs. 25–28); **a, f** right lateral view of carapace with parts of right valve exfoliated, exposing the internal mold and the outer surface of the inner lamella of the multi-laminar valve; note faint comarginal concavity seen on the surface of the exposed inner lamella (arrow in **a**); **d** left lateral view

showing v-shaped dent in carapace and wrinkled appearance of posterodorsal parts of carapace; **h** dorsal view (anterior up). **b, c, e, g** PMU22584, paralectotype, right and left lateral views (**b** and **e**) and dorsal view (**c** anterior up) showing partly exfoliated and dented carapace; **g** detail of **b** showing punctate ultrastructure of carapace. Scale bar equals 2 mm except in **g** (1 mm)

Indiana anderssoni (Wiman, 1903)

Figure 5a–h

1893 *Leperditia* n. sp., ähnlich *Leperditia* (*I*) *dermatoides* Walcott—Wiman: p. 69.

v * 1903 *Aparchites?* *Anderssoni* n. sp.—Wiman: p. 45–46, 57, pl. 1, figs. 25–28.

1931 *Aparchites?* *anderssoni* Wiman, 1905 [sic]—Kummerow: p. 251, fig. 6.

1931a *Indiana anderssoni* (Wiman, 1902) [sic]—Ulrich and Bassler: p. 72, pl. 9, figs. 22–25 (re-illustration of figures of Wiman 1903).

Material studied. Type series of Wiman (1903), comprising eight specimens from erratic boulder no. 3 collected on Eggegrund Island, Gävle Bay, southern Gulf of Bothnia. Of the eight specimens in the type series, only two represent complete, presumably adult specimens. The remaining specimens are either incomplete and poorly preserved juveniles or indeterminate carapace fragments. The description below is based on these two complete specimens, as only they can unambiguously be assigned to *Indiana anderssoni* (PMU22583, PMU22584).

Type material. Wiman (1903) did not select a holotype and illustrated only a single specimen (a complete carapace) as a line drawing. The specimen on which this drawing was based is selected here as the lectotype (PMU22583, Fig. 5a, d, f, h). The second complete specimen is assigned to be a paralectotype (PMU22584, Fig. 5b, c, e, g).

Diagnosis. Medium-sized species of *Indiana* (adults ca. 5 mm long) with moderate postplete carapace, punctate ultrastructure, and straight to gently convex dorsal margin. Length of straight hinge line slightly longer than half of carapace length. Anterior margin rounded and somewhat pointed.

Description. Lectotype and paralectotype are similar in size, with the latter being slightly larger, measuring 4.70 mm and 5.15 mm in length, 3.02 mm and 3.27 mm in height, and 1.9 and 2.1 mm in width, respectively. The hinge line measures 2.48 mm and 2.67 mm, respectively, equivalent to 52% of carapace length. Outline moderately postplete, with straight to gently convex dorsal margin bearing straight hinge line (Fig. 5b). Posterodorsal margin straight or nearly so, with transition to dorsal margin smooth, enclosing a posterior cardinal angle of ca. 136–138°. Anterodorsal margin straight to gently convex, slightly more than half as long as posterodorsal margin. Anterodorsal and posterodorsal curves indistinct, creating an evenly rounded free margin, but with anterior margin somewhat pointed. Carapace ultrastructure punctate (Fig. 5g) and multilamellar (Fig. 5a); carapace of lectotype slightly thickened in a zone parallel and close to the free margin.

Discussion. The overall outline and size of *Indiana anderssoni* is most similar to the type species of *Indiana*, *I. lippa*, from the middle Cambrian Dugald Formation of Avalonian Nova Scotia. *I. lippa* is distinguished by having

a smooth, not punctate, carapace and a broader rounded anterior free margin. *Indiana secunda* from the (uppermost lower Cambrian) Hanford Brook Formation of Avalonian New Brunswick has a punctate ultrastructure and a pointed anterior margin like *I. anderssoni*, but is comparatively more strongly postplete in outline. Likewise, *I. dermatoides* from lower Cambrian limestones of Laurentian New York State is distinguished from *I. anderssoni* in being markedly postplete. In addition, *I. dermatoides* has a shorter hinge line in relation to carapace length (see also the “Discussion” of the genus *Indiana* above).

There is a general misperception regarding the year of publication of Wiman’s article that includes the description of *I. anderssoni*. Ulrich and Bassler (1931a) state that *I. anderssoni* was published in 1902, whereas other authors cite the article as 1903 (e.g., Williams et al. 2007; Nielsen and Schovsbo 2011; Peel and Streng 2015) or 1905 (e.g., Kummerow 1931; Williams and Siveter 1998; Streng et al. 2008). The correct date is 1903, when it was first published as an individual article which was later integrated into the sixth volume of the *Bulletin of the Geological Institution of the University of Upsala*. This volume was published in 1905 and includes 13 articles individually published between 1902 and 1905 (J.O.R. Ebbestad, pers. comm. 2018).

Occurrence. Uppermost lower Cambrian (Cambrian Stage 4) of Sweden.

“*Indiana minima* Wiman, 1903”

Figure 6a–c

v * 1903 *Indiana? minima* n. sp.—Wiman: p. 48–49, 57, pl. 1, figs. 38, 39.



Fig. 6 Specimen described as *Indiana minima* by Wiman (1903) from an erratic boulder found on Åland, Finland, PMU22606, interpreted herein as a flattened ellipsoidal phosphatic grain rather than a fossil. **a** Perpendicular view of exposed flat side of grain showing two marks at edge of grain (arrows) and unevenly distributed “tubercles” representing tips and edges of silt-sized mineral grains embedded in phos-

phatic groundmass; specimen coated with a sublimate of ammonium chloride to augment texture. **b** Same view as in **a** but without coating showing natural color and shiny surface of grain. **c** Lateral view of exposed flat side of grain showing marks at edge of specimens and “tubercles” in profile. Scale bar equals 1 mm

1931 *Indiana? minima* Wiman, 1905 [sic]—Kummerow: p. 252, fig. 10.

1931a *Indiana? minima* Wiman, 1902 [sic]—Ulrich and Bassler: p. 83, pl. 9, fig. 14 (re-illustration of figures of Wiman 1903).

Material studied. Only known specimen from Wiman's collection (PMU22606); from erratic boulder no. 1 (glauconitic sandstone) collected in Jomala parish north of Lumparn, Åland Islands (Finland), entrance to the Gulf of Bothnia.

Description. Overall, the specimen is dark black in color with a shiny and reflective surface. It has an evenly rounded oblate ellipsoidal shape, measuring 1.2 mm in length, 0.8 mm in height, and is at least 0.2 mm wide. Its surface is smooth, except for some irregularly distributed tiny knobs and two minor marks providing some positive and negative relief, respectively. Knobs are the result of silt-sized mineral grains being imbedded in and sticking out from the black, most likely phosphatic, groundmass of the specimen. The two small marks (arrows in Fig. 6a) are irregular in outline and have a slightly rougher texture than the remaining surface.

Discussion. The original description of *Indiana minima* is based on a single specimen which was found within a block of sandstone, a glacial erratic from Fasta Åland, the largest of the Åland Islands, Gulf of Bothnia. The facies of the block in combination with the co-occurrence of *Torellella laevigata* most likely indicate an early Cambrian age (see also Nielsen and Schovsbo 2011). The erratic host rock is a poorly sorted glauconitic fine-grained sandstone which includes coarse quartz grains up to 1.5 mm in size.

Features of *Indiana minima* mentioned by Wiman (1903) include a flattened shape, lack of sculpture, and a black shiny chitinous shell. Judging from the original description and illustrations, Ulrich and Bassler (1931a) considered that Wiman's species was unlikely to belong to *Indiana* because of its rounded outline and small size. Kummerow (1931) seems to have seen and studied the specimen, as he mentions that the shell is not completely smooth, as stated by Wiman (1903), but has unevenly distributed tubercles ("...mit einigen verstreuten Tuberkeln besetzt," Kummerow 1931, p. 252). Our re-study of the specimen confirms Wiman's and Kummerow's morphological observations, but we consider the specimen to represent an inorganic phosphate grain with inclusions of silt-sized mineral grains. Tips and edges of these mineral grains stick out of the black phosphatic groundmass, producing the tubercles mentioned by Kummerow (1931) (compare Fig. 6a, c). No sutures, hinges, or systematic ornamentation have been observed which would indicate that the specimen is a shell. It seems to be a flattened

grain with evenly rounded edges that entirely consists of phosphate, as indicated by the two small marks. Accordingly, we consider that *Indiana minima* does not represent a fossil; it should be considered a *nomen dubium*.

Genus *Indota* Öpik, 1968

Type species. *Indota otica* Öpik, 1968, p. 19, pl. 1, figs. 1–4 (by original designation), from the "Yelvertoft Beds" of the Thornton Limestone, Ordian, Queensland, Australia.

Diagnosis (modified after Siveter and Williams 1997). Medium to large bradoriids (adults about 10 mm long) with an elongate, postplete carapace characterized by a lateral, shallow furrow parallel to, but some distance from, the free margin of valve; dorsal margin straight, about two-thirds to three-quarters of valve length; valves granulose or smooth.

Discussion. The diagnosis of the genus generally follows Siveter and Williams (1997), but a length of the dorsal margin of "about two thirds of valve length" (Siveter and Williams 1997, p. 34) appears to be too narrowly formulated. This diagnosis fits the type species *I. otica*, but Laurence and Palmer (1963) state a ratio between the length of the hinge and length of the valve of 0.8 for their specimens of *Indota tennesseensis* (Resser, 1938). Judging from illustrated specimens, the ratio appears to be somewhat lower though, i.e., ca. 0.72 (Laurence and Palmer 1963, fig. 73.2, see also Siveter and Williams 1997, pl. 4, fig. 5). The diagnosis has accordingly been broadened slightly.

Siveter and Williams (1997, p. 36) surprisingly placed *Indota otica* in synonymy, although questionably, with *I. tennesseensis*. In their opinion, both taxa show "no fundamental difference in size and morphology." However, *I. tennesseensis* reaches lengths of up to 10 mm (Laurence and Palmer 1963), contrasting with a maximum length of only 5 mm for *I. otica* (Öpik 1968). More importantly, both species are also clearly dissimilar in shape, with *I. tennesseensis* being moderately postplete and thus contrasting with the strongly postplete outline of *I. otica*, which has its greatest height beyond the posterior cardinal angle (Öpik 1968). *Indota otica* and *I. tennesseensis* are here considered to be two geographically, stratigraphically, and morphologically distinct species.

When Resser (1938) introduced *Indota tennesseensis*, he compared his new species with *Indiana labiosa* Ulrich and Bassler, 1931a from the middle Cambrian Stephen Formation in British Columbia, Canada. According to Ulrich and Bassler (1931a, p. 79), *I. labiosa* is characterized by a "broad flattened ventral rim," a feature that could suggest reference to *Indota*. However, this rim appears to be present in only one of the two specimens assigned to the species (Ulrich and Bassler 1931a, pl. 9, fig. 27 vs. fig. 26), and two different

taxa might have originally been illustrated under the same name. In their review of the bradoriids of North America, Siveter and Williams (1997) re-evaluated *I. labiosa* and recognized that only one of the two specimens still existed and was available for study (USNM 56464, Ulrich and Bassler 1931a, pl. 9, fig. 26). This remaining specimen lacks the flattened brim and was considered indeterminate by Siveter and Williams (1997), but was questionably assigned to *Dielymella* by Williams et al. (2007, fig. 6.4). The lost specimen might have been closer to *Indota* than to *Indiana*.

Indota formosa, described by Fleming (1973) from the middle Cambrian (Templetonian Regional Stage) Beetle Creek Formation of the Georgina Basin, Australia, has a concave posterodorsal margin and possibly a triangular anterior sulcus (compare Fleming 1973, fig. A7) indicating an affinity with the family Comptalutidae Öpik, 1968. Features of a rather large specimen from the same formation referred to as *Indota* sp. by Fleming (1973) are difficult to evaluate. The specimen is strongly compressed but its dorsal margin shows a possible cusp (Fleming 1973, pl. 1, fig. 13), which is representative of the family Cambriidae.

The holotype of *Indota acuta* Zhang, 1986 from the lower middle Cambrian (Wuliuan Global Stage) of Hainan Island, China shows similarities with *Indota*, but the vertical anterodorsal margin and a seemingly developed cusp on the anterior part of the dorsal margin suggest reference to *Matthoria* Siveter and Williams, 1997. The lower Cambrian (Botoman/lower part of Cambrian Stage 4) *Indota usloniensis* Mel'nikova, 1988 from Kazakhstan is a comptalutid and was assigned to *Alutella* Kobayashi and Kato, 1951 by Mel'nikova et al. (1997), but tentatively referred to *Houlongdongella* Li, 1975 by Zhang (2007). A single specimen from the Atdabanian (Cambrian Stage 3) of central Kazakhstan has been illustrated as *Indota?* sp. by Mel'nikova et al. (1997) (see also Williams et al. 2007). The specimen appears to have an anterior sulcus, an admarginal ridge, and a pronounced anterodorsal curve—features not reminiscent of *Indota*. It could represent a relatively large deformed (axially elongated) comptalutiid or svealutid.

Two early middle Cambrian specimens described and illustrated by Jones and Kruse (2009) as *Indota?* sp. from the Georgina Basin, Australia are from the same lithostratigraphical unit as the type species *I. otica*. The two specimens are poorly and incompletely preserved, but one of the specimens shows a well-defined comarginal brim and seems to preserve a distinctly elevated anterior? lobe (Jones and Kruse 2009, fig. 14A). Outline, comarginal brim, and expressed lobe suggest reference to the family Beyrichonidae Ulrich and Bassler, 1931a or to certain hipponicharionids, such as *Pseudobeyrichona* Shu, 1990a.

Peel and Willman (2018) illustrated two specimens from the lower Cambrian Buen Formation of North Greenland, which they questionably assign to *Indota*. The first specimen

(Peel and Willman 2018, fig. 9F) agrees in shape and size with *Indota*, but the characteristic comarginal groove does not seem to be developed. The other specimen, an incomplete left valve (Peel and Willman 2018, fig. 9G) shows a faint comarginal concave zone, but only anteroventrally. Restudy revealed faint pore-like structure in the first specimen, potentially indicative of a punctate ultrastructure. The concave zone in the second specimen might be analogous to what is seen in *Indiana anderssoni*. Both specimens are considered here to be closer to *Indiana* than to *Indota*.

Species included. Type species and *Indota tennesseensis* (Resser, 1938) (see also the “Discussion” above).

Occurrence. Upper lower Cambrian (Cambrian Stage 3) of eastern Laurentia (eastern Tennessee, USA) and lower-middle Cambrian boundary interval (Ordian Regional Stage; Cambrian Stage 4) of East Gondwana (northwestern Queensland, Australia) (see Siveter and Williams 1997); questionably from the lower middle Cambrian of western Laurentia (Delamaran Regional Stage; Wuliuan) and the middle Cambrian (Agdzian Regional Stage) of West Gondwana (Germany) (herein).

Indota? sp.

Figure 7a–e

Material. Single incomplete carapace with only right valve fully exposed, specimen SSMM 5688, from the Wildenstein Member of Tannenknock Formation, sample locality W8.

Description. Exposed part of carapace shows a large right valve, measuring 11 mm in length and 6 mm in height, slightly asymmetrical in lateral view, subamplete to slightly postplete in outline. Valve strongly convex in transverse section, with highest point close to dorsal margin, resulting in a steep dorsal slope and a less inclined ventral slope. Ventral slope flattens close to the free margin. Accordingly, a flattened area is present along the free margin, being broadest posteriorly and narrowest anteriorly, measuring ca. 11% and 5% of valve length, respectively. Free margin evenly rounded without distinct anterodorsal or posterodorsal curve. Dorsal margin deformed, slightly concave in lateral view with primarily straight hinge line broken up into segments (Fig. 7b); dorsal margin measures about 80% the length of the carapace. Part of anterior margin of carapace fully exposed, revealing presence of at least parts of left valve (Fig. 7d).

Discussion. The most distinctive feature of *Indota?* sp. is its relatively large size, measuring 11 mm in length, and the absence of any lobation. Bradoriida comparable in size have been described from the families Bradoriidae (e.g., *Indiana*), Svealutidae (e.g., *Anabarochilina* Abushik, 1960),

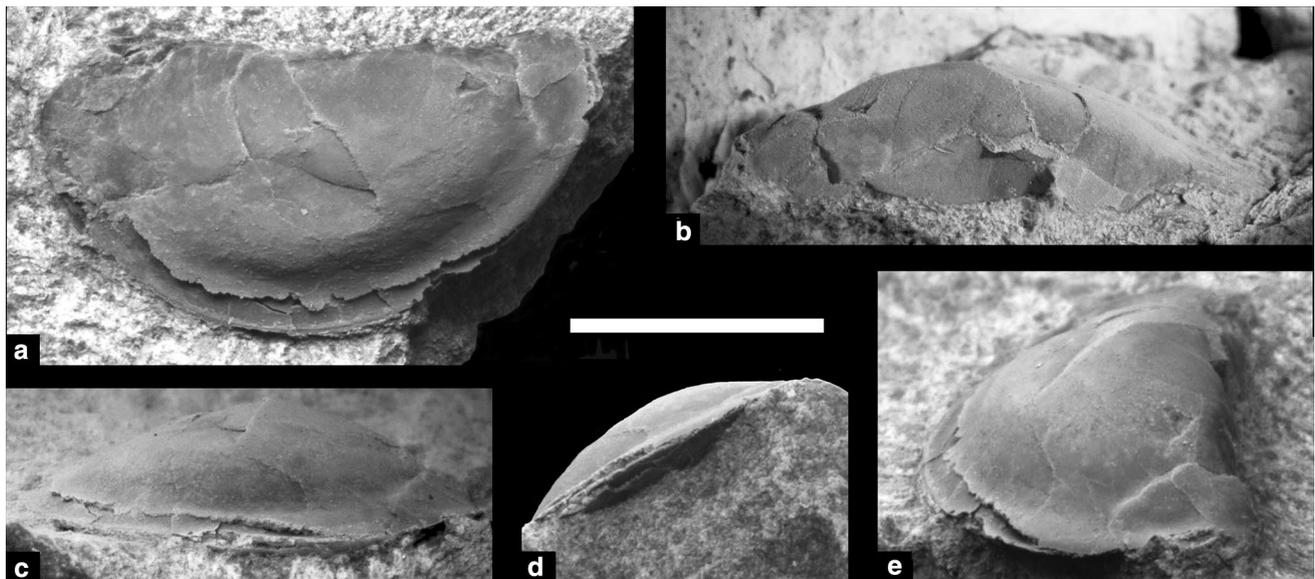


Fig. 7 *Indota?* sp., specimen SSMM 5688, Tannenknock Formation, Wildenstein Member, sample locality W8. **a–c** Lateral, dorsal, and ventral views of exposed right valve. **d** Exposed anteroventral mar-

gin suggesting the presence of an opposing valve. **e** Oblique anterior view. Scale bar equals 5 mm

and Cambriidae (e.g., *Petrianna* Siveter, Williams, Peel and Siveter, 1996) (Siveter et al. 1996; Siveter and Williams 1997; Hou et al. 2002), as well as for individual genera whose affiliations are unclear, i.e., *Mononotella* Ulrich and Bassler, 1931a and *Dielymella* Ulrich and Bassler, 1931a. Lobation is absent in certain genera of the family Bradoriidae (*Indiana* and *Indota*), might be poorly developed in certain svealutids such as *Liangshanella* or *Ovaluta*, and is not developed in some genera of unclear systematic placement (e.g., *Mononotella*, *Dielymella*). Svealutids are characterized by a distinct admarginal ridge and furrow which is not developed in *Indota?* sp. *Mononotella* has a univalved carapace and *Dielymella* has a distinct anterocardinal spine and a punctate ultrastructure (Ulrich and Bassler 1931a; Siveter and Williams 1997). Size and absence of lobation, as well as other characters of *Indota?* sp. such as smooth carapace, subamplete to postplete outline, and straight hinge line, fit best with the family Bradoriidae, primarily the two genera *Indiana* and *Indota*. Typical species of *Indiana*, however, have a hinge line that measures 40% to two-thirds of the carapace length. The hinge line in *Indota?* sp. is significantly longer, ca. 80% the length of the carapace. *Indota* can have a hinge line comparable in length to that of *Indota?* sp. (Laurence and Palmer 1963) and is also characterized by a lateral furrow that extends along the free margin. The flattened area of *Indota?* sp. is reminiscent of this lateral furrow. Although no clear furrow is developed in *Indota?* sp., the concave flexure of the carapace, i.e., the change from the convex central part of the carapace to the flattened marginal part,

is in an equivalent position to the furrow in *Indota*. In other aspects, *Indota?* sp. is most similar to the moderate postplete Laurentian *I. tennesseensis* (Resser, 1938) from the lower Cambrian Murray Shale in eastern Tennessee. *Indota?* sp. differs from *I. tennesseensis* in having a somewhat longer hinge line, a rounded rather than straight posterodorsal margin, and a lower length–width ratio.

Some carapaces from the lower Cambrian of South China, originally described as various species of *Mononotella* Ulrich and Bassler, 1931a (see, e.g., Huo and Shu 1985 or overview in Huo et al. 1991) recall *Indota* and *Indota?* sp. The species *Mononotella subquadrata* Jiang, 1982 and *Mononotella chuanshaanensis* Huo and Shu, 1985 appear to have a comarginal structure similar to the groove seen in *Indota*. *Mononotella longa* Huo and Shu, 1985 lacks this groove but its other characters (such as size, length–width ratio, overall outline, and length of hinge line) are reminiscent of *Indota?* sp. from the Franconian Forest. Remarkably, all three species (among others) have subsequently been considered to be within the morphological variability of a single species, *Chuandianella ovata* (Li, 1975), which is not a bradoriid but a waptiid arthropod (see Huo and Bergström 1997). Hence, it is possible that *Indota?* sp., with its somewhat unusual proportions, also does not represent a bradoriid, but is the carapace of a larger bivalved arthropod. Many other early and middle Cambrian bivalved arthropods such as *Waptia*, *Perspicaris*, or *Canadaspis* have a morphologically simple carapace with a relative long hinge line which is similar in

outline and size to that of *Indota?* sp. However, the strong mineralization and thickness of the carapace of *Indota?* sp., in combination with its seemingly closed-bivalved preservation, would be an unlikely state of preservation for the typically delicate, poorly, or non-mineralized carapaces of such arthropods (e.g., Vannier et al. 2018).

Occurrence. *Ornamentaspis frequens* Biozone, Agdzian Regional Stage, probably coeval with the earliest part of the Wuliuan; Franconian Forest (northeastern Bavaria, Germany). West Gondwana.

Family **Hipponicharionidae** Sylvester-Bradley, 1961

Diagnosis (modified after Siveter and Williams 1997, p. 44). Small to medium-sized Bradoriida (adults ca. 1–6 mm in length) with carapaces being subamplete to postplete or somewhat preplete, subtriangular to semicircular in outline; dorsal margin straight with well-developed hinge line. Tri- to multilobate; anterior and posterior lobes typically strongly developed, may be discrete or ventrally fused to form connecting lobe. Trilobate forms have small to indistinct central lobe situated adjacent to dorsal margin and anteriorly of valve mid-length. Multilobate forms with up to seven ventrally confluent lobes. Admarginal ridge entire.

Genera included. *Pseudobeyrichona* Cui in Shu, 1990a; *Flumenoglacies* Peel and Streng, 2015, and *Navarana* Peel, 2017 in addition to genera listed in Williams et al. (2007).

Discussion. *Pseudobeyrichona* Cui in Shu, 1990a was questionably synonymized with *Neokunmingella* Zhang, 1974 by Hou et al. (2002), which is not followed herein (see the “Discussion” of *Pseudobeyrichona* below). For other potential synonymy, see Hou et al. (2002).

Genus ***Pseudobeyrichona*** Cui in Shu, 1990a

- 1987 *Beyrichona*. Cui et al., p. 75.
 1990a *Pseudobeyrichona* [Cui] gen. nov.—Shu, p. 47.
 1990b *Pseudobeyrichona* Shu 1987 [sic]—Shu, p. 322. [but see Malz 1990]
 1991 *Beyrichona*—Huo et al., p. 167.
 1993 *Pseudobeyrichona* Shu, 1990a—Hinz-Schallreuter, p. 422.
 1997 *Pseudobeyrichona* Cui, in Shu, 1990a—Siveter and Williams, p. 48.
 1998 *Pseudobeyrichona* Cui (in Shu 1990a)—Williams and Siveter, p. 15.
 2007 *Pseudobeyrichona* (Cui, 1987) [sic]—Zhang, p. 147.
 2009 *Pseudobeyrichona* Shu, 1990a—Jones and Kruse, p. 64.

Type species. *Pseudobeyrichona longquanxiensis* Cui in Shu, 1990a (holotype NWUX D44505; Shu 1990a, pl. 6, fig. 1a, 1b) from the Shuijingtuo Formation (Cambrian Stage 3), Xiaoyangba section, Zhenba County, southern Shaanxi, China. The type species is considered to be a junior subjective synonym of *Beyrichona longquanxiensis* Cui in Cui et al., 1987 (holotype NWUX S84022; Cui et al. 1987, pl. 1, fig. 22) from the Shuijingtuo Formation, Longquanxi section, Goaqiao, Pengshui County, Chongqing municipality, China. As a consequence, *Pseudobeyrichona longquanxiensis* Cui in Shu, 1990a becomes a junior secondary homonym (ICZN 57.3.1) of *Pseudobeyrichona longquanxiensis* (Cui in Cui et al., 1987) (see the “Discussion” below for details).

Emended diagnosis (modified and extended after Zhang 2007). Small hipponicharionid (adults ca. 1.5–2 mm in length) with subtriangular, postplete carapace typified by moderately to weakly developed anterior and poorly elevated posterior lobe; central lobe absent or indistinct. Most anterior point of carapace at anterior end of hinge line or close to it. Anterior and posterior curves poorly developed; valves inflated ventrally. Admarginal ridge narrow, seemingly continuous between cardinal corners, becomes indistinct posterodorsally.

Discussion. As indicated by Hinz-Schallreuter (1993, p. 422) and Zhang (2007, p. 147–148), there is a certain degree of taxonomic confusion with respect to the genus *Pseudobeyrichona* and its type species. Whereas the genus is typically attributed to “Shu, 1990” (e.g., Hinz-Schallreuter 1993, 2006; Hou et al. 2002; Jones and Kruse 2009), it has also been credited to “Cui in Shu, 1990” (Siveter and Williams 1997; Williams and Siveter 1998), “Shu, 1987” (Shu 1990b), “Cui in Cui et al., 1987” (Hinz-Schallreuter 2006), and “Cui, 1987” (Zhang 2007). The type species is quoted as *Pseudobeyrichona longquanxiensis* (Cui, 1987) in Zhang (2007), but the same combination of genus name and species epithet has also been attributed to, e.g., “Cui in Shu, 1990,” “Cui 1985,” or “(Cui et al., 1987),” among others (see synonymy list of *Pseudobeyrichona longquanxiensis* below).

When the genus *Pseudobeyrichona* was introduced in Shu (1990a, p. 47), the type species was stated to be “*Pseudobeyrichona longquanxiensis* Cui gen. et sp. nov.,” which was directly followed by the description of the new species under the heading “*Pseudobeyrichona longquanxiensis* Cui gen. et sp. nov.” (Shu 1990a, p. 48). This means that in Shu (1990a), both the new genus as well as its type species were attributed to Cui in two instances. Accordingly, the author of *Pseudobeyrichona* and its type species should be “Cui in Shu, 1990a” as stated by Siveter and Williams (1997) and Williams and Siveter (1998).

Confusingly, Cui (in Cui et al. 1987) had already described a morphologically alike species with the same

species epithet, i.e., *Beyrichona longquanxiensis* from the Longquanxi section in Pengshui County, China. Hence, it is probable that Shu (1990a) intended *B. longquanxiensis* Cui, 1987 to be the type species of his new genus but formulated his intentions incorrectly. However, the two species must be considered separate taxa (see also Hinz-Schallreuter 1993), as the publication by Cui et al. (1987) is not cited in Shu (1990a), and as two different specimens were assigned as holotypes for *Pseudobeyrichona longquanxiensis* (NWUX D44505; in Shu 1990a) and *Beyrichona longquanxiensis* (NWUX S84022; in Cui et al. 1987). Hinz-Schallreuter (1993) hypothesized that *B. longquanxiensis* and *P. longquanxiensis* might be conspecific. She suggested that *Pseudobeyrichona* might be a junior synonym of *Albrunnicola* Martinsson, 1979, but only assigned *B. longquanxiensis* to *Albrunnicola*. However, she subsequently considered *Pseudobeyrichona* to be a valid genus (Hinz-Schallreuter 2006). Hou et al. (2002) questionably synonymized *Pseudobeyrichona* with *Neokunmingella* Zhang, 1974 and mentioned a possibly synonymy of *B. longquanxiensis* and *P. longquanxiensis*. Zhang (2007) considered *Pseudobeyrichona longquanxiensis* Cui in Shu, 1990a and *Beyrichona longquanxiensis* Cui in Cui et al., 1987 to represent the same species, which is followed herein. However, with the transfer of *B. longquanxiensis* to *Pseudobeyrichona*, *B. longquanxiensis* becomes a secondary homonym of the type species of *Pseudobeyrichona*, *Pseudobeyrichona longquanxiensis* Cui in Shu, 1990a, b. The status of *Pseudobeyrichona longquanxiensis* Cui in Shu, 1990a as the type species of *Pseudobeyrichona* (ICZN Article 67.1.2.) remains unchanged, but it is theoretically necessary to propose a new name to replace *Pseudobeyrichona longquanxiensis* (Cui in Shu, 1990a) if *Beyrichona longquanxiensis* Cui in Cui et al., 1987 is subjectively assigned to *Pseudobeyrichona*. As this new name would be placed immediately in synonymy with *Pseudobeyrichona longquanxiensis* (Cui in Cui et al., 1987), we refrain from proposing a new name.

The genus *Pseudobeyrichona* was initially placed within the family Beyrichonidae Ulrich and Bassler, 1931a (Shu 1990a), but was listed without further explanation under the family Hipponicharionidae in Shu (1990b). Hinz-Schallreuter (1993) argued that *Pseudobeyrichona* is more likely a member of the Hipponicharionidae than the Beyrichonidae, close to or synonymous with *Albrunnicola*. A hipponicharionid rather than beyrichonid affinity was also suggested by Williams and Siveter (1998). By tentatively synonymizing *Pseudobeyrichona* with *Neokunmingella*, Hou et al. (2002) might have implied a hipponicharionid affinity of *Pseudobeyrichona* as well. Zhang (2007) also claimed placement of *Pseudobeyrichona* within the Hipponicharionidae but, based on the study of new material, he considered the genus to be legitimate and distinct from *Albrunnicola* as well as *Neokunmingella*.

The inadequately known *Beyrichona zhenbaensis* described by Tong in Huo et al., 1991 from the same section and formation as *P. longquanxiensis* (Xiaoyangba section of the Shuijingtuo Formation) is referred to *Pseudobeyrichona* herein. The species has poorly elevated lobes like *P. monile* sp. nov. and an outline similar to *P. longquanxiensis*. It is distinguished in having a more distinctly developed posterodorsal curve and a less steep comarginal ramp. However, restudy of the holotype might show that it is synonymous with *Pseudobeyrichona longquanxiensis* (Cui in Cui et al., 1987).

Pseudobeyrichona biluddensis described by Hinz-Schallreuter (2006) from the lower Cambrian of Sweden is characterized by a postplete carapace with long, distinctly elevated anterior and posterior lobes. Lobes are narrow and run parallel to the free margin, separated ventrally by a narrow gap. Although *P. biluddensis* is similar in size and outline to *Pseudobeyrichona*, the distinctness of its lobes on a rather flat valve suggest reference to *Hipponicharion* Matthew, 1886 rather than *Pseudobeyrichona*.

Species included. *Beyrichona longquanxiensis* Cui in Cui et al., 1987, *Beyrichona zhenbaensis* Tong in Huo et al., 1991, and *Pseudobeyrichona monile* sp. nov.

Occurrence. Lower Cambrian (Cambrian Stage 3) of South China (Shuijingtuo Formation, Chongqing municipality and Shaanxi province) (e.g., Cui et al. 1987; Shu 1990a, b; Huo et al. 1991; Zhang 2007) and lower middle Cambrian (Agdzian Regional Stage) of West Gondwana (Bavaria) (herein).

Pseudobeyrichona longquanxiensis (Cui in Cui et al., 1987)

1987 *Beyrichona longquanxiensis* Cui sp. nov.—Cui et al., p. 75, pl. 4, figs. 22–24.

1987 *Beyrichona longquanxiensis* Cui et Huo, sp. nov. [sic]—Cui et al., p. 77.

1990a *Pseudobeyrichona longquanxiensis* Cui gen. et sp. nov.—Shu, p. 48, pl. 6, figs. 1–7; ?text-fig. 24.

1990b *Pseudobeyrichona longquanxiensis* Cui 1985 [sic]—Shu, pl. 2, figs. 25, 26.

1991 *Beyrichona longquanxiensis* Cui 1987—Huo et al., p. 167, pl. 32, figs. 18–20.

2007 *Pseudobeyrichona longquanxiensis* (Cui, 1987)—Zhang, p. 148–149, pl. 18, figs. 9–19, text-fig. 4I, J.

2008 *Pseudobeyrichona longquanxiensis* (Cui in Cui et al., 1987)—Zhang and Pratt, fig. 2A–D.

2014 *Pseudobeyrichona longquanxiensis* (Cui and Huo, 1987) [sic]—Yang, fig. 10 M.

2015 *Pseudobeyrichona longquanxiensis* (Cui et al., 1987) [sic]—Yang et al., fig. 10 M.

Diagnosis (modified after Zhang 2007, p. 148–149). Species of *Pseudobeyrichona* with distinctly elevated to spinose anterior lobe and poorly elevated posterior lobe. Marginal rim narrow; surface smooth or partially wrinkled.

Occurrence. Lower Cambrian (Cambrian Stage 3) of South China (Shuijingtuo Formation, Chongqing municipality and Shaanxi Province).

***Pseudobeyrichona monile* sp. nov.**

Figure 8a–e

Holotype. Specimen MMUW 2018A-002. Composite? phosphatic mold of a single right valve (only available specimen).

Locus typicus. Sample horizon W8, small farm road just east of a small abandoned quarry, Wildenstein slice, Franconian Forest, northeastern Bavaria, Germany (see Appendix).

Stratum typicum. *Ornamentaspis frequens* Biozone, Agdzian Regional Stage (probably coeval with the earliest part of the Wuliuan), Wildenstein Member of Tannenknock Formation, lower middle Cambrian.

Etymology. After the Latin *monile*, meaning necklace; a reference to the series of small tubercles that form the admarginal ridge.

Diagnosis. Species of *Pseudobeyrichona* with weakly developed lobes and coarsely crenulated admarginal ridge.

Description. Single known specimen distinctly postplete, measuring 2.2 mm in length and 1.7 mm in height. Lateral outline subtriangular, characterized by straight dorsal margin, measuring ca. 88% of shell length, and evenly rounded free margin in the shape of a horizontally sheared “U.” Accordingly, free margin lacks pronounced postero- and anterodorsal margins, anterior curve is not developed, and posterior curve is indistinct and posteroventrally situated. Dorsal and free margin enclose an angle of 110° posteriorly and ca. 65° anteriorly. Well-defined admarginal ridge developed along free margin and separated from lateral parts of valve by narrow furrow. Ridge ca. 60 μm broad and characterized as being coarsely crenulated. Lobation of valve poorly expressed; narrow anterior lobe faintly elevated at anterodorsal margin, posterior lobe broader but indistinct, both confluent with inflated ventral part of valve; central lobe vestigial and situated anterocentrally, close to dorsal margin. Lateral parts of valve steep due to proximity of anterior and posterior lobes to admarginal ridge and inflated ventral part of valve. Valve surface smooth.

Discussion. The imperfect preservation of the specimen leaves some characters of *Pseudobeyrichona monile* sp. nov. unresolved. Both cardinal corners are incomplete and parts of the admarginal ridge are lacking anterodorsally.

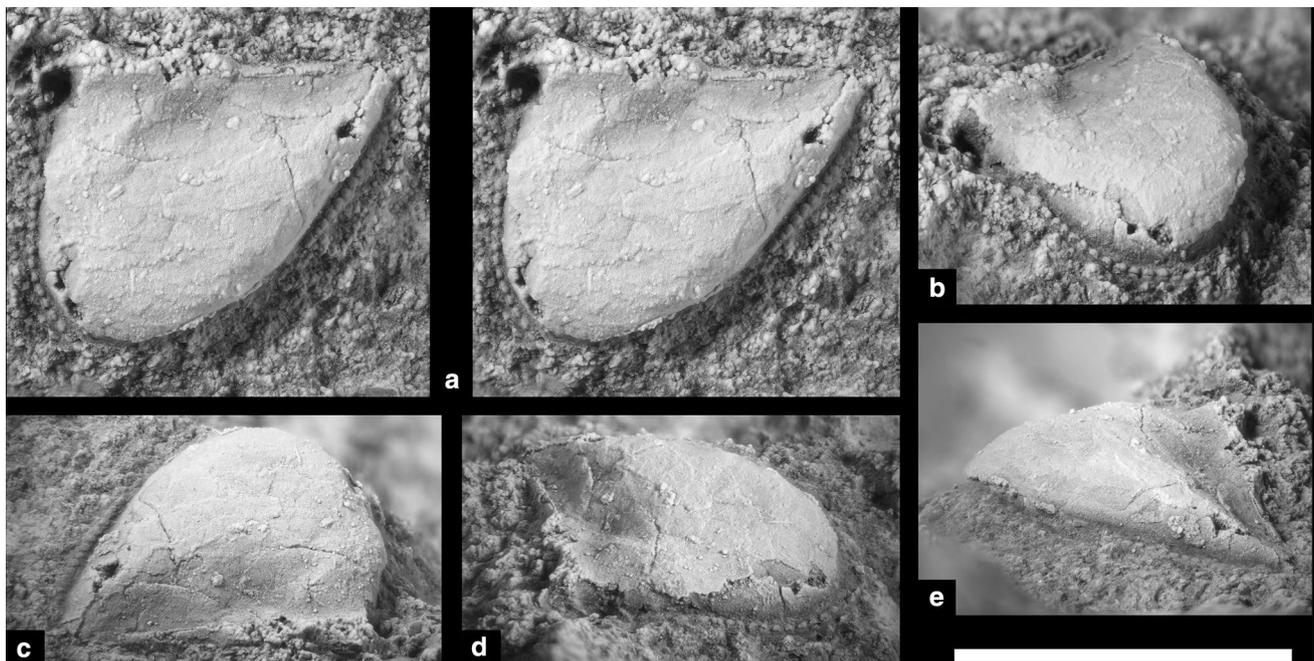


Fig. 8 *Pseudobeyrichona monile* sp. nov., holotype, MMUW 2018A-002, right valve; Tannenknock Formation, Wildenstein Member, sample locality W8. **a** Stereo pair of valves in lateral view; **b** oblique posteroventral view showing crenulated admarginal ridge; **c–e** oblique dorsal, posterior, and anterior views. *Scale bar* equals 2 mm

Hence, it is unclear if the ridge extends entirely between the cardinal corners and if a short anterodorsal margin with a frontal extremity, analogous to *P. longquanxiensis*, was developed or not. A hole on the anterior lobe of *P. monile* might suggest the presence of a spine similar to that of *P. longquanxiensis*, adults of which show an anterior lobe with a spine-like anterodorsal extension. However, the hole in *P. monile* appears to be taphonomic rather than related to the morphology of the valve.

P. monile sp. nov. differs from other species of *Pseudobeyrichona* by its poor lobation and its unique crenulated admarginal ridge. A superficially similar ridge is described in the genus *Mannocosmia* Zhang, 1986, which is typified by a row of tubercles that extends between the cardinal corners, parallel to the free margin. However, the ridge in species of *Mannocosmia* is not situated marginally as in *P. monile* but close to the margin of the shell, and might be equivalent to ventrally fused anterior and posterior lobes rather than an admarginal ridge.

Family **Svealutidae** Öpik, 1968

Diagnosis. See Siveter and Williams (1997).

Genera included. *Melvilleella* Wrona, 2009 in addition to genera listed in Williams et al. (2007) (see also Zhang 2007 and the discussion in Peel et al. 2016).

Svealutidae gen. et sp. indet.

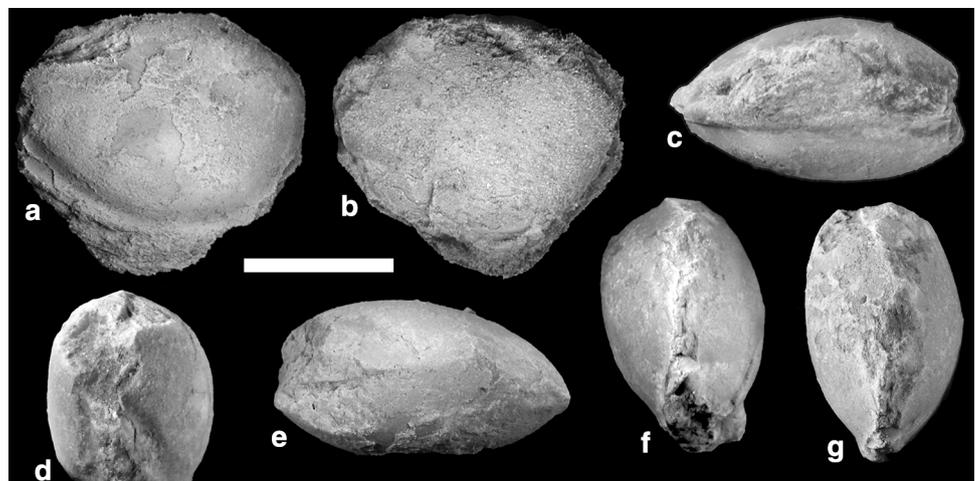
Figure 9a–e

Material. Single anteriorly and posterodorsally incomplete carapace, SSMM11815; from the Triebenreuth Formation of the Schnebes–Wustuben slice near Elbersreuth/Wustuben, Franconian Forest.

Description. The specimen as preserved measures 9.5 mm in length and 7.4 mm in height and has a width of ca. 5.2 mm. Both valves are strongly convex with a postplete outline. The preserved posterior part of the dorsal margin is straight and encloses an angle of ca. 144° with the seemingly straight posterodorsal margin. Free margin of left valve partly preserved ventrally and anteroventrally, showing a ca. 0.5 mm broad comarginal brim. No ornamentation or lobation observed on the seemingly smooth carapace surfaces.

Discussion. All measurements refer to the incomplete specimen. Hence, the angle between dorsal and posterodorsal margins might have originally been different, as the specimen most likely had an entire comarginal brim which is not preserved along the posterodorsal margin. Whereas the measured height and width would represent the actual dimensions of the original carapace, the measured length of 9.5 mm does not include the missing posterior and anterior marginal brim and large parts of the anterior carapace. Thus, the original length of the carapace was probably 11–12 mm. This relatively large size, in combination with the strong convexity of the valve and the presence of a comarginal brim suggest an affinity to the Svealutidae. However, the incomplete preservation of the specimen with systematically important parts missing (i.e., the anterior part of the shell, including a substantial part of the dorsal margin) allow merely a tentative assignment to this family. Preserved characters, such as the smooth carapace in combination with a comarginal brim, would also match certain cambriids (e.g., *Matthoria*) and some comptalutids (e.g., *Alutella* or *Comptaluta* Öpik, 1968). However, the carapace of *Matthoria* has its maximum width anteriorly rather than centrally and comptalutids are smaller (<3 mm; e.g., Hou et al. 2002). Furthermore, the Bavarian specimen does not show any indication of a dorsal cusp or anterodorsal sulcus characteristic for the cambriids and comptalutids, respectively.

Fig. 9 Svealutidae gen. et sp. indet., SSMM 11815-I, from the Triebenreuth Formation, sample locality S1; carapace with outer layers partly exfoliated. **a, b** Left and right lateral views of carapace; **c** ventral view; **d** anterior view showing incomplete preservation; **e** dorsal view with partly preserved hinge line; left and right valves slightly twisted against each other, causing asymmetric appearance of carapace; **f, g** posterior and posterodorsal views. Scale bar equals 5 mm



Hence, an assignment to the Svealutidae appears to be the most parsimonious placement for the Bavarian specimen, and the observed characters might indicate relationships to genera such as *Liangshanella* or *Anabarochilina*.

Summary

A new fauna of bradoriids from the traditional lower middle Cambrian (Akdzian Regional Stage, probably late Cambrian Stage 4 through Wuliuan) of the Franconian Forest is described. The recognized bradoriids belong to families characteristic of West Gondwana (Bradoriidae, Hipponicharionidae, and Svealutidae), but the assigned genera (i.e., *Indiana*, *Indota*, and *Pseudobeyrichona*) are all previously unknown from the area. In total, five different species from three stratigraphic units have been distinguished: *Indiana* sp. from the Galgenberg Member of the Tannenknock Formation, *Indiana* aff. *dermatoides* (Walcott), *Indota*? sp., *Pseudobeyrichona monile* sp. nov. from the Wildenstein Member of the Tannenknock Formation, and an undetermined svealutid from the Triebenreuth Formation.

Indiana (Family Bradoriidae) is a genus typical of the lower Cambrian (Cambrian Series 3 and 4) of Laurentia, Avalonia, and Baltica (Fig. 10). Wuliuan occurrences are

rare and have so far been restricted to two coeval occurrences in Eastern Avalonia (upper Wuliuan, *Eccaparadoxides etemincus* Biozone = *Hartella bucculenta* Biozone) (Siveter and Williams 1997). The specimens of *Indiana* from the Wildenstein Member represent the third middle Cambrian occurrence of the genus and fill a gap in its stratigraphic distribution. Four specimens from the Franconian Forest have been assigned to *Indiana*, but a conclusive specific identification was not possible. The two better preserved specimens are best compared with *I. dermatoides*, known from the lower Cambrian of eastern Laurentia, but have a less distinct postplete outline and might represent a new species.

The genus *Indota* (Family Bradoriidae) is known only from two geographically widely separated areas in northwestern Australia and eastern Laurentia (Fig. 10). A discovery of the genus in western Gondwana as a geographically intermediate position may indicate a rare but cosmopolitan distribution of the genus. However, the material from the Franconian Forest could not confidently be assigned to *Indota*. The single specimen shows characters typical of the family Bradoriidae, where it is closest to *Indota*. Similar to the comarginal groove typical for *Indota*, *Indota*? sp. shows a comarginal concavity which separates a broad marginal area from the remainder of the carapace. Nevertheless, the comarginal structure as well as the carapace outline are quite

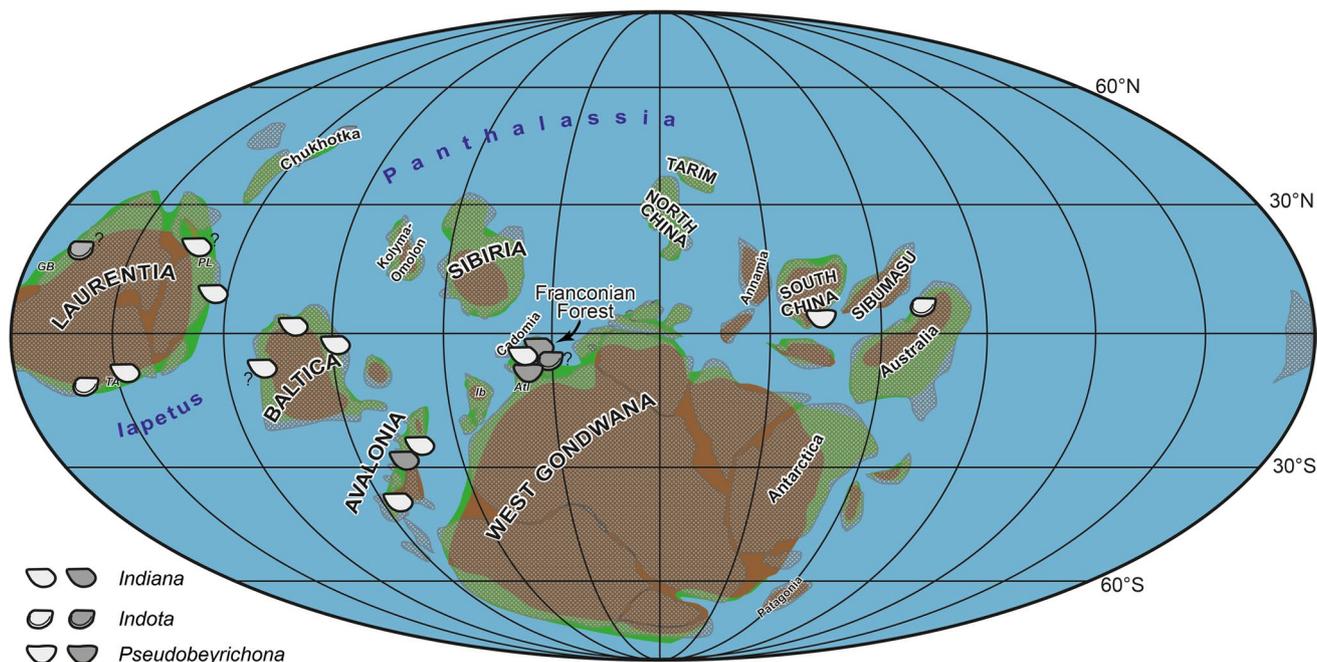


Fig. 10 Regional distribution of the genera *Indiana*, *Indota*, and *Pseudobeyrichona* during Cambrian Stages 3–4 (white symbols) and during the Wuliuan (gray symbols); questionable occurrences are indicated by a question mark. Paleogeographic map represents the early Wuliuan [map modified from Malinky and Geyer (in press,

fig. 1), based on data modified from Dalziel (1997), Scotese and McKerrow (1990), and McKerrow et al. (1992)]. *Atl* Moroccan Atlas Ranges, *GB* Great Basin region, *Ib* Iberia, *PL* Peary Land, Greenland, *TA* Taconic Allochthon

different from the known species of *Indota*, and it is more likely that *Indota?* sp. represents a new genus and species.

Pseudobeyrichona (Family Hipponicharionidae) is a genus known from the lower Cambrian (Cambrian Series 3) of the South China continent. The occurrence of the new species *P. monile* extends the geographic and stratigraphic distribution of the genus (Fig. 10) and corroborates previous reports of typical “eastern” taxa in western Gondwana. A crenulated admarginal ridge as seen in *P. monile* is a feature previously unreported from the Bradoriida.

Svealutid bradoriids show a global distribution. Nevertheless, the supposed svealutid from the Franconian Forest is only the second report of this family from western Gondwana. The preserved features of the carapace are reminiscent of the widespread genera *Liangshanella* and *Anabarochilina*.

In addition to the description of the new fauna, the regional distribution, morphological variability, and diversity of the genera *Indiana*, *Indota*, and *Pseudobeyrichona* have been reviewed. As a result, the diagnoses of *Indiana* and *Indota* have been modified and the diagnosis of *Pseudobeyrichona* emended. The genus *Indiana* now comprises six species with *Indianites ovooides* from the lower Cambrian of Baltica added as a distinct species of *Indiana*. The upper lower Cambrian species *Indiana anderssoni* and *Indiana minima*, two poorly known taxa from Baltica, are re-described and re-illustrated. *Indiana anderssoni* has been shown to be a species of *Indiana*, whereas the problematic “*I. minima*” is identified as a pseudo-fossil. In contrast to *Indiana*, only two species can confidently be recognized within the genus *Indota*. The two species have previously

been synonymized but are herein considered to be geographically, stratigraphically, and morphologically distinct species. *Pseudobeyrichona* is considered a distinct genus that, in addition to the type species, comprises *Beyrichona zhenbaensis* as well as the new species *P. monile*.

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Appendix

See Table 1.

Table 1 Samples facies relevant for this study

Sample ID	Trilobite biozone	Lithostratigraphic unit	Tectonic unit	Coordinates	Collector(s)
W2	<i>Kingaspidoidea frankenwaldensis</i> Biozone	Tannenknock Formation, Galgenberg Member	Wildenstein slice	50°11'47"N 11°33'29"E	Meier
W8	<i>Ornamentaspis frequens</i> Biozone	Tannenknock Formation, Wildenstein Member	Wildenstein slice	50°11'58"N 11°33'36"E	Meier, Sdzuy
W12	<i>Kingaspidoidea frankenwaldensis</i> Biozone	Tannenknock Formation, Galgenberg Member	Wildenstein slice	50°12'15"N 11°33'45"E	Geyer, Meier, Sdzuy
W13b	<i>Ornamentaspis frequens</i> Biozone	Tannenknock Formation, Wildenstein Member	Wildenstein slice	50°12'17"N 11°33'33"E	Meier
S1	Probably <i>Badulesia tenera</i> Biozone	Triebenreuth Formation	Schnebes–Wustuben slice	50°15'0"N 11°34'20"E	Meier

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