Dating of Cambrian–Ordovician boundary strata in northernmost Vietnam and methodological aspects of evolutionary biostratigraphic inference

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ABSTRACT: Unrepeatability of evolution and the correspondence of the fossil record to ancestor-descendant successions of species are the unavoidable, although usually hidden, assumptions in any reliable age determination based on fossils. We expose these assumptions while dating early Paleozoic carbonate rock deposits in the Lung Cu section at the Vietnamese–Chinese border. The best-preserved and most abundant fossils in this section are shumardiid trilobites. The succession of shumardiid species, based on data from elsewhere, provides an evolutionary reference standard. The shumardiid record is not sufficiently complete to verify hypotheses of ancestor-descendant relationships but enables estimation of the 'degree of evolutionary advancement' of the Vietnamese species. This suggests an age close to the Cambrian–Ordovician boundary. Although considered non-scientific by cladists, such inferences are testable. Support for a late Furongian or early Tremadocian age is provided by the occurrence of *Cordylodus* conodonts in strata above the trilobite-bearing bed. The conodont evolution has a good fossil record interpreted in population terms in the Baltic region and Australia, including the lineage represented in Vietnam. Age determination based on such evolutionary reasoning is reliable but of a relatively low resolution, because the rate of morphological evolution is generally low. Generally, more precise dating is offered by distribution of fossils controlled by ecological factors, which are repeatable and mostly diachronous over large geographic distances, but they may have happened relatively rapidly. The appearance of the *Iapetognathus*-*Chosonodina*-bearing conodont assemblage in the Lung Cu area, as suggested by its occurrences elsewhere, was probably due to abrupt faunal migration into the region.

INTRODUCTION

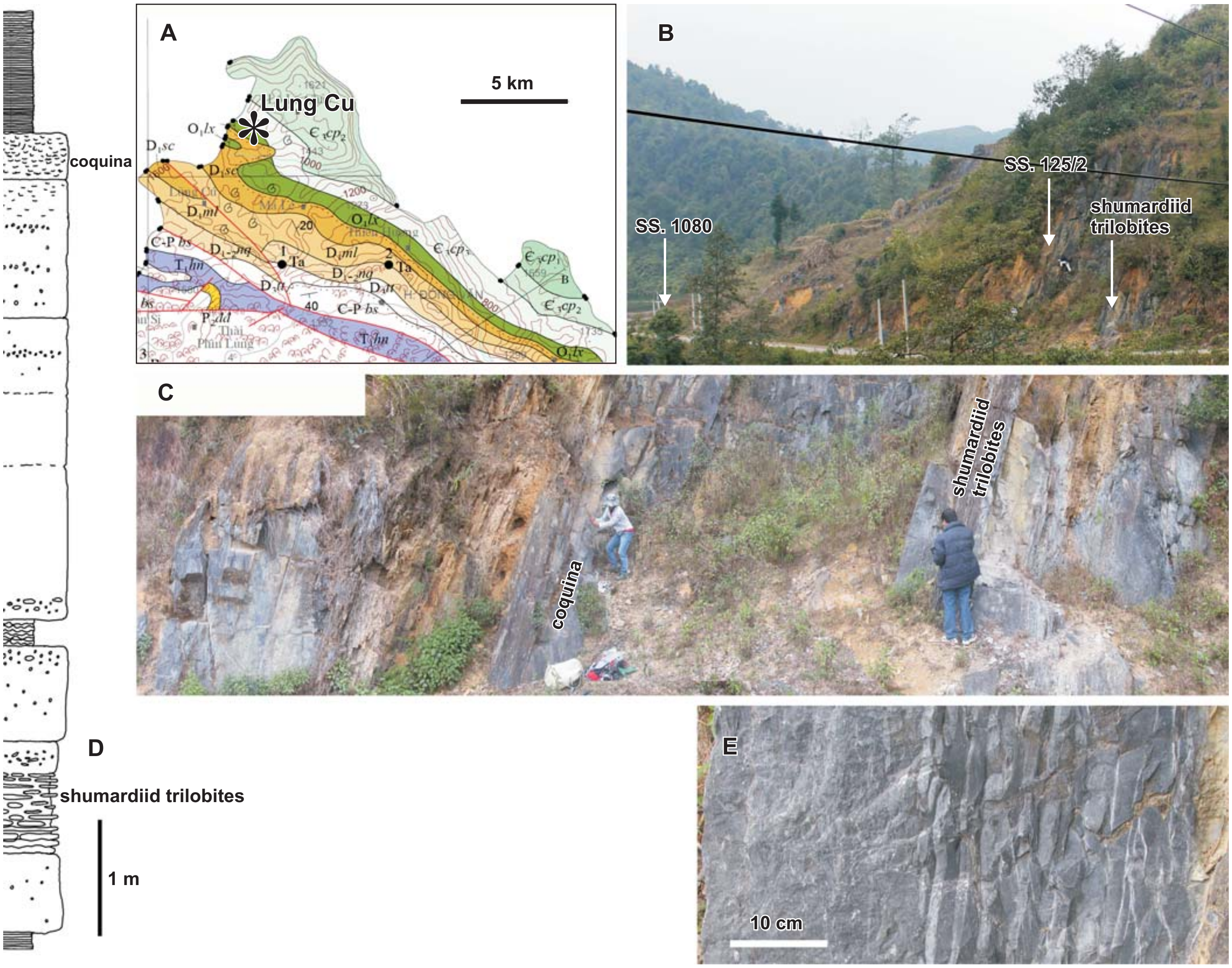
Temporal calibration of phylogenies requires evidence from the fossil record. This results in a significant, although rarely acknowledged, conflict between the methodological approaches of biostratigraphy and phylogenetics that has implications also for related research in biology. Cladistic analysis simply evaluates relationships between taxa independent of time, whereas biostratigraphy commonly infers ancestor-descendant relationships (discussed, e.g., by Dzik 2005, 2015; Wickström and Donoghue 2005). Owing to a similar methodological discrepancy, the nature of correspondence between the succession of fossils and definitions of geochronological units is among the most controversial issues in geology. Contemporaneity of strata from multiple sites is usually inferred by identifying ranges of the same species (or higher rank taxa). The crucial point is the meaning of correlation lines that are results of such inferences—do they represent unrepeatable evolution of organisms or are they just an expression of repeatable and possibly diachronous control by local ecological factors?

These fundamental aspects of biostratigraphic methodology are of minor importance in everyday practice and are rarely considered, so much so that in today's reality of geological research any proposal of correlation is entangled in countless facts and interpretations compiled by earlier students of the same subject. Discussed in this study, pristine sedimentary successions at the northernmost tip of Vietnam host important assemblages of early Palaeozoic invertebrates. Because of the complex political history of the region, its geological mapping and stratigraphy has remained at a rather basic level for decades (e.g., Deprat 1915a, 1915b, 1916; Mansuy 1915a, 1915b, 1916; Kobayashi 1944; Dovzhikov 1965) and has only recently been re-evaluated (Tinh 1976; Tinh et al. 2001; Ngân and Huöc 1996; Ngân 2008; Huyen et al. 2007; Thanh & Khuc 2011). Here we use evidence mainly from trilobite and conodont assemblages to resolve the age of the strata at Lung Cu and expose some methodological problems with the dating of evolutionary events and sedimentary strata using fossils.

GEOLOGICAL SETTING

The Lung Cu section is adjacent to the Vietnamese–Chinese border at Lung Cu village, 23 km north of Dong Van District Town, at the northernmost tip of Vietnam (text-fig. 1; 23°21' 15"N; 105°17'38"E). This region belongs to the South China terrane (Stokes 2008; Krobicki et al. 2008), which was part of the Yangtse continent. The strata exposed in this section are composed mostly of steeply dipping carbonate beds (i.e., micritic and oolitic limestone, locally dolomitic) interbedded with shale, marlstone, siltstone and sandstone.

Two samples near the top of the succession mapped as Ordovician yielded a few conodont elements and one contained numerous silicified trilobite exoskeletons. The conodonts derive from a coquina of orthoid brachiopods (text-fig. 1B) that are too fragmentary and diagenetically altered for taxonomic identification. The coquina also yielded crudely silicified unidentifiable trilobite exoskeleton fragments, phosphatic linguliform brachiopods



TEXT-FIGURE 1
A, Location of the Lung Cu section (asterisk) on the geological map of the Dong Van area in northernmost Vietnam. Abbreviations: ϵ_2-ϵ_3 cp, Chang Pung Formation (Upper Cambrian); O_1 *lx*, Lutxia Formation (Lower Ordovician); D_1 *sk*, Si Ka Formation (Lochkovian); D_1 *bb*, Bac Bun Formation (Lochkovian–Pragian); D_1*ml*, Mia Le Formation (Pragian); $D_{1\text{-}3}$ *sp*, Si Phai Formation (Pragian–Frasnian); D_3 *tt*, Toc Tat Formation (Frasnian–Famennian); C-P*bs*, Bac Son Formation (Carboniferous–Permian); P_3*dd*, Dong Dang Formation (Upper Permian) T_1 *hn*, Hong Ngai Formation (Lower Triassic). **B**, Photograph of the outcrop with location of productive samples. **C**, View of the abandoned quarry showing relationship between the brachiopod coquina and limestone concretions with the shumardiiid trilobites. **D**, Position of the fossiliferous beds on the diagrammatic rock column. **E**, Enlargement of the bed with concretions containing silicified shumardiid trilobites.

and internal moulds of probable bellerophontid gastropod larval shells.

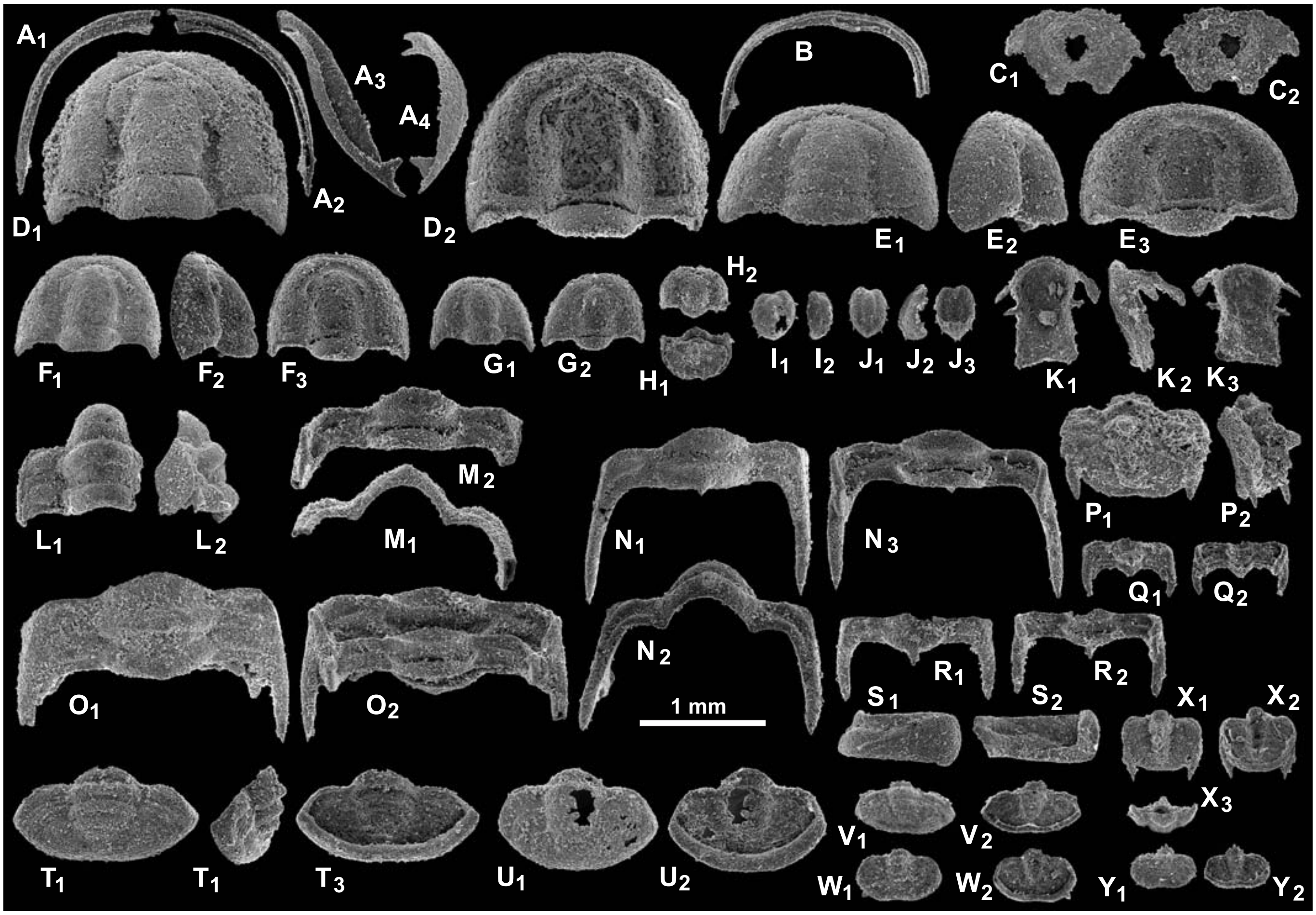
Relatively well preserved but low-diversity silicified trilobites were extracted from flat limestone concretions occurring in a stratigraphically lower marl bed. Trilobites are of great importance in discussions on the palaeogeography of Indochina (Gonzalo et al. 2003; Stokes 2008) and we focus our research on them.

MATERIAL

The shumardiid trilobite material consists of 98 cranidia, 48 librigenae, two of them still attached to cranidia and 6 hypostomes (two attached), 169 thoracic tergites probably representing all segments of the thorax, and 54 pygidia. Twenty one specimens represent the protaspis stage, without the distinction between cephalon and pygidium yet developed. The sample is monospecific (with the exception of the fragmentary specimen in text-fig. 2C).

Only two samples (2 kg) were productive for conodonts: five elements were found in the brachiopod coquina (one represents *Teridontus*, others *Cordylodus*), four in sample SS 1080, taken about 30 m above the coquina (*Cordylodus, Semiacontiodus*, *Iapetognathus*, and *Chosonodina*).

The materials discussed in this paper are housed at the Institute of Paleobiology, Polish Academy of Sciences, in Warsaw (abbreviated ZPAL).



TEXT-FIGURE 2
Silicified exoskeleton elements of the shumardiid *Conophrys* sp. extracted from limestone concretions (A, B, D–Y) and probable partial cranidium or hypostome of unidentified trilobite ZPAL V.47/5 (C).

A	Right half of fused free cheeks (librigenae) ZPAL V.47/23 in ventral (A1), dorsal (A2), inner lateral (A3) and oblique outer lateral (A4) views.
B	More complete cheeks ZPAL V.47/22 in dorsal view.
D–G	Cranidia ZPAL V.47/69, 3, 64, and 62 of various ontogenetic ages in dorsal, ventral and lateral views.
H	Coiled complete early meraspis ZPAL V.47/15 seen from its cephalon and pygidium.
I,J	Protaspides ZPAL V.47/17 and 18 in dorsal, ventral and lateral views.
K	Hypostome ZPAL V.47/6 in ventral, lateral and dorsal views.
L	Two first thoracic tergites ZPAL V.47/53 in dorsal and lateral views.
M,N	Macropleural third tergites ZPAL V.47/21 and 33 in ventral, posterior, and dorsal views.
O	Tergites 3–5 ZPAL V.47/20 preserved together in dorsal and ventral views.
P,X	Pygidia and associated thoracic segments ZPAL V.47/14 and 16 of early meraspides.
Q,R	Spinose macropleural tergites ZPAL V.47/19 and 8 of late meraspides. S. Right pleura ZPAL V.47/7 of post-macropleural tergite.
T–Y	Pygidia ZPAL V.47/10, 9, 11, 12 and 13 of various stages in dorsal, lateral and ventral views.

QUANTITATIVE EVOLUTIONARY PALAEOBIOLOGY VS. BIOSTRATIGRAPHY

Modern biostratigraphy and quantitative evolutionary palaeobiology use ranges of taxa observed in rocks as the basic empirical evidence. Stratigraphic ranges of species or higher taxa are easy to quantify and analyse statistically. However sophisticated and rigorous are methods used to produce biostratigraphic correlation lines (e.g., Sadler 2004) their actual meaning remains a controversial issue. This is because homotaxy does not imply synchronous events (e.g., Scott 1985). Instead, such lines connect the same stage of ecological transformation of communities at different geographic points and would be isochronous only if the controlling factor acted isochronously (e.g., Dzik 1995).

The main controlling factor that determines appearances or disappearances of fossil species is taphonomy, the second in importance is ecology. There is little chance that an appearance of fossils in the rock corresponds to the evolutionary origin of a species (e.g., Dzik 1997, 1999a, 1999b, 2002, 2006). Despite this rather obvious aspect of the observed ranges, they continue to be the basic units for quantitative paleobiology since the classic works of Simpson (1944) and the influence of the 'Sepkoski curve', which is probably the best exemplification of this attitude (e.g., Sepkoski 1996), on modern palaeobiology can hardly be overestimated. Ironically, the recent expansion of the philosophy of cladistics to areas of classical stratigraphy-based palaeontology has appeared unexpectedly destructive to this approach. Instead of treating the fossil record as an expression of the process of evolution, with its temporal dimension, cladistics concentrates its interest on patterns in the distribution of morphologic characters, being a modern approach to the search for the non-evolutionary 'natural' system of classification (cf. Stevens 2013). Eventually, the 'evolutionary' approach to taxonomy is being contested and replaced with a 'cladistic' one, defined on hypothetical divergences of lineages, not on the extent of morphological diversity. But the duration of such taxa does not reflect the rate of morphological evolution or diversity, which was the purpose of compilation of the 'Sepkoski curve'.

An even more serious problem with the application of cladistics to data of biostratigraphic importance is what value should be given to geological time and space distances between fossil samples. Cladists construct parsimonious patterns of relationships based on morphology alone assuming equal value of characters (or giving them a value *a priori*). Unavoidably, morphological characters (unlike molecular ones) are arbitrarily defined and chosen. Geological time is not allowed as the ordering factor. There is no point at which stratigraphy-based evolutionary inference based on ancestor-descendant relationships (chronophyletic; Dzik 2005) or dense sampling (stratophenetics; Gingerich 1979) meets with cladistics. Results of cladistic inference on evolutionary relationships among extinct organisms can be evaluated with stratigraphic evidence only after the most parsimonious networks of relationships based on morphology alone are calibrated with geological time to become chronograms (e.g., Bell and Lloyd 2015). As no ancestor-descendant relationship is allowed in chronograms, taxa originate invariably by dichotomy (or polytomy), which results in long 'ghost lineages', not represented in the fossil record. Because it is assumed that all evolution is concentrated in (allopatric) speciation events, most of the evolution is by definition hidden in dichotomies (polytomies), being out of reach of palaeontology. These are aspects of cladistic chronograms that alone may cause controversies, but probably even more intriguing is the way in which temporal data used to calibrate chronograms are obtained. Ironically, the main, if not only, source of it is biostratigraphy. But in biostratigraphy, the estimate of 'evolutionary advancement', although criticized as non-scientific by cladists, typically remains the only reliable way to use fossils in geological age determination.

Below, an approach alternative to that based on ranges of taxa is exemplified by using fossil evidence on a single occurrence of a species to determine geological age of the source rock. It does not matter how many species are considered, but how fast they evolve. This requires a reference standard—a hypothesis of ancestor-descendant succession within the lineage, to which the species used for such dating belongs. We will present such inference first for a trilobite species from the Lung Cu section and then the result of dating will be tested by conodonts from the overlying beds.

BIOSTRATIGRAPHIC INFERENCE

The Lung Cu trilobites

A complete set of sclerites of the trilobite exoskeleton are represented among about four hundred specimens freed from the flat limestone concretions with formic acid (text-fig. 2). This enabled restoration of the whole exoskeleton (text-fig. 3). All specimens are more or less tectonically deformed. This makes biometric analysis meaningless but there is little doubt that cephalic and pygidial shapes are very variable within the sample.

Protaspides are cordiform, with a depression in front of the incipient glabella (text-fig. 2I, J). They are covered with sharp spines and it is possible that this kind of ornamentation was also present in later ontogenetic stages, being obscured by crude silicification.

Cranidia of individuals more advanced in ontogeny are strongly convex, both in transverse and sagittal planes. On the ventral side, the posterior branch of the facial suture delimits the cephalic doublure that gradually narrows until it reaches the occipital ring; it then expands, covering almost the whole ring with a concave inner blade (text-fig. $2D_2$). The fused cheeks are widest in the middle of their anterior-posterior dimension (text-fig. 2A). This trilobite was blind.

The hypostome has a concave anterior margin (text-fig. 2K), which does not fit the convex margin of the doublure of the cheeks. This means that the hypostome was freely suspended in unmineralized cuticle (natant; Fortey and Chatterton 1988). Despite this, at least two specimens preserved their hypostomes *in situ*. Their preservation does not allow the details of their relationship to the cheeks (possibly fused together with the rostral plate) to be seen. The anterior part of the hypostome is strongly convex and almost hemispherical. The two prominent wings are developed on each side of the hypostome—antennae passed between them.

The articulating half-ring of the first thoracic tergite is prominent (text-fig. 2L). Both the first and second tergite have flat pleurae with rounded contours, apparently an adaptation to enrollment. These two thoracic segments are preserved in articulation but the morphology of the third segment remains unknown. Fragmentary pleural spines of much smaller length than those of the macropleural fourth segment may belong to this location in the thorax. The macropleural tergites are well represented in the material. Their articulating half-rings are rather short, corresponding to the extent of the inner lamella on preceding segments. The length of pleural spines increased during ontogeny (compare text-fig. 2P, Q and N) but remained variable. The medial spine is the most prominent in advanced meraspides (text-fig. 2R) but is very short or even missing in the mature stage (holaspis; text-fig. 2O). The two last segments are preserved in articulation (text-fig. 2O) and they have blunt ventral tips of pleurae with a rather narrow doublure (text-fig. 2S).

Four rings are well developed on mature pygidia. A doublure of uniform width extends along their posterior margin (text-fig. 2T, U).

The peculiar anterolateral glabellar lobes and lack of eyes clearly indicate the Shumardiidae, which was widely distributed in late Cambrian and Ordovician open-sea bottom environments.

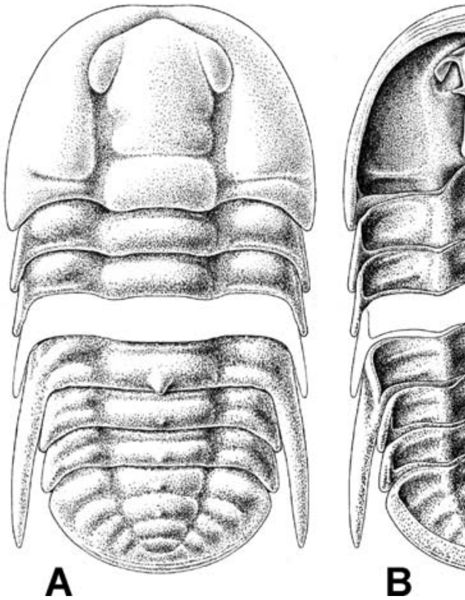
Evolutionary reference standard

The recent review of late Cambrian to late Ordovician Shumardiidae by Waisfeld et al. (2001) reveals notable changes in exoskeleton spinosity and glabella complexity through time (text-fig. 4). Most of the recorded members of the family are known from a single bed in just one locality each. However, it seems obvious that these are snapshots from a continuum of evolving populations (anagenesis) undergoing allopatric speciation events (phylogenesis) from time to time.

The origin of the Shumardiidae remains unknown. The latest middle Cambrian *Oculishumardia hunania* Peng et al. (2003) was proposed as intermediate between the ptychoparioids and shumardiids (Peng et al. 2003) but this has been questioned by Park et al. (2008). The oldest well-known shumardiids are represented by a series of probable chronospecies of *Elaphraella* from the middle Furongian Sesong Formation of Korea (Park and Choi 2012), the youngest is probably *Shumardia polonica* from the Late Ordovician (late Katian) of Poland (Kielan 1960). *Elaphraella* had long genal spines and macroplurae. The oldest species, *E.*? *taebaeksanensis* Park and Choi (2012), has a sinuous facial suture which indicates the possible presence (or presence in its immediate ancestor) of eyes in the anterior part of the cranidia.

The presence of small eyes was proposed by Peng (1993) for *Akoldinioidia dydimacantha* from the late Cambrian Bitiao Formation of Hunan, China, but questioned by Park and Choi (2012) who regarded the alleged palpebral lobes as an artifact, not an original structure. The age of this shumardiid is probably middle Furongian (Park and Kihm 2015). *Koldinioidia choii* and *Akoldinioidia lata* from the Hwajeol Formation of Korea immediately succeeded *Elaphraella* (Park and Kihm 2015). The late Furongian *Koldinioidia orientalis* lacks macropleurae but bears a prominent occipital spine (Zhu and Peng 2006) and is probably the oldest shumardiid with recognizable anterolateral glabellar lobes.

Other early shumardiids had only one (fourth) macropleural segment. The early Tremadocian *Acanthopleurella grindrodi* had reduced its postmacropleural segments (and mature size; Fortey and Rushton 1980). The thorax is known in few shumardiids and the timing of disappearance of macropleurae in the of *Shumardia granulosa* lineage (Whittington 1965) is unknown. They are absent in the latest Floian *S. gadwensis* (Fortey and Owens 1987). The opposite trend is represented in the evolution of the *Leoforteya hintzei* lineage, the oldest shumardiid with genal spines (Waisfeld et al. 2001). Genal spines became as long as the macropleural spines in the late Darriwilian to Sandbian clade of *Changchowilla* and *Kweichowella* (Waisfeld et al. 2001).

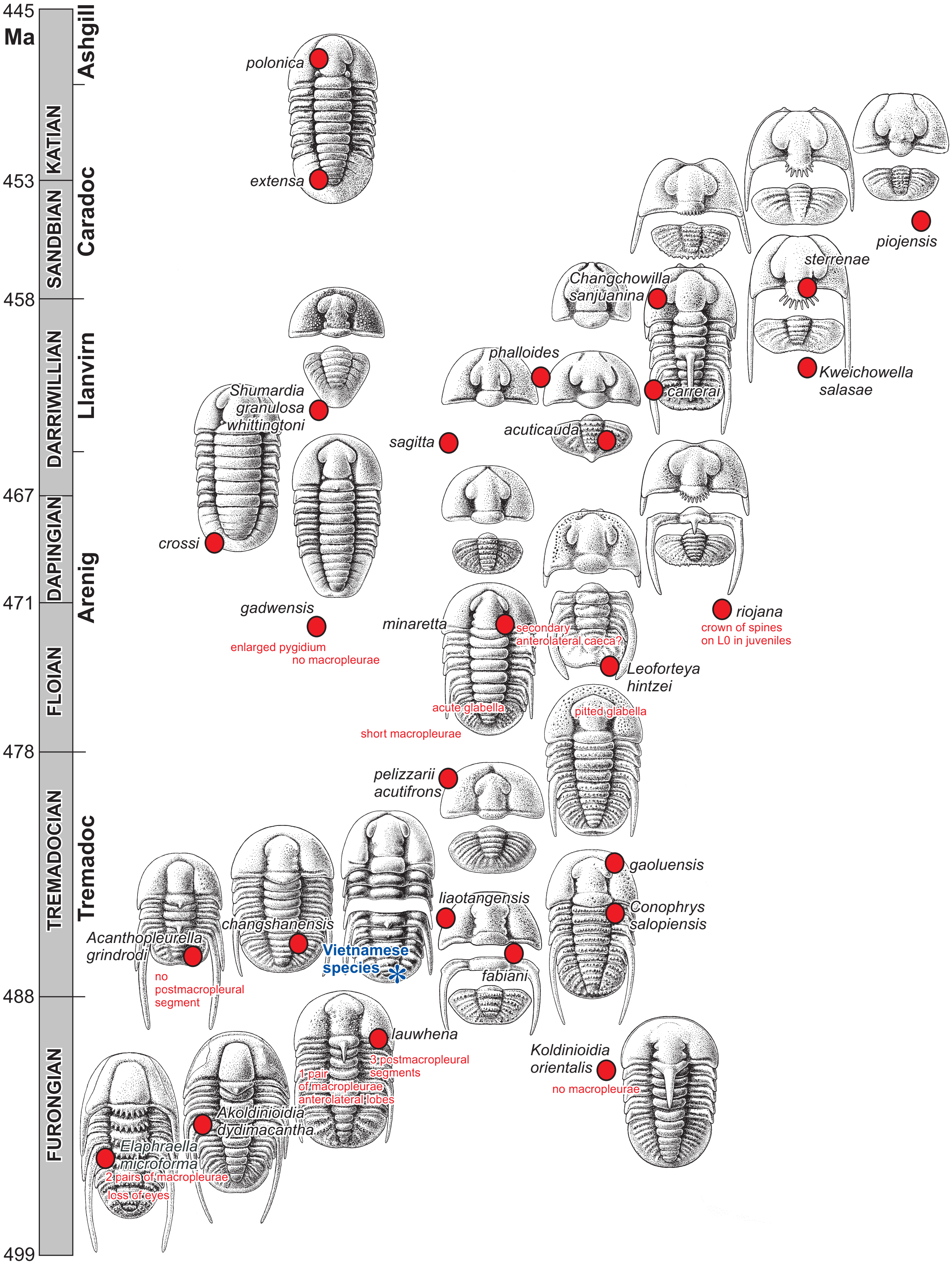


TEXT-FIGURE 3
Restoration of *Conophrys* sp. exoskeleton from the Lung Cu section in dorsal (A), and ventral (B) views.

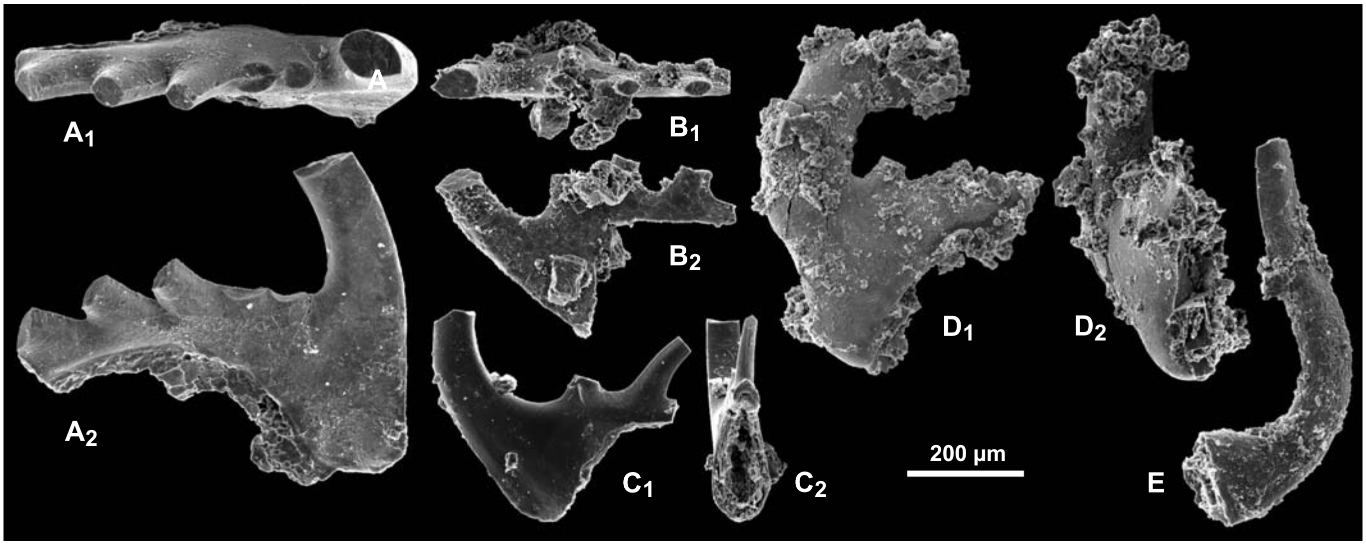
No such derived aspects of the exoskeleton morphology are represented in the Vietnamese shumardiid. Unless it was an Ordovician ‘living fossil’, it must be not younger than Tremadocian. It also lacks the advanced features of pygidium morphology and ornamentation that characterize the late Tremadocian *Conophrys salopiensis* from the Shineton Shale, Shropshire, England (Fortey and Rushton 1980) the Scandinavian *C. pusilla* (Fortey and Owens 1991; Ebbestad 1999), as well as the early Tremadocian *C. changshanensis* from Hunan, China, and *C. fabiani* from Salta, Argentina, which have a bordered, elevated, and tuberculate posterior of the pygidium (Lu and Lin 1984; Peng 1984; Waisfeld et al. 2001). The Vietnamense species resembles ‘*Shumardia*’ *liantangensis* from the early Tremadocian of Zhejiang, China (Lu and Lin 1984) in its gently convex pygidium but the different state of preservation (in shale) makes closer comparison difficult.

If the Vietnamese species truly belongs to the lineage of *Conophrys liantangensis*, the most likely age of the bed with limestone concretions exposed at Lung Cu is early Tremadocian.

The strata immediately below and above the trilobite-bearing concretionary bed lack determinable fossils. The trilobite-bearing bed apparently corresponds to one of the brief episodes of relative sea-level rise (Lehnert et al. 2005), and continues into a high-energy deposit with concretions reworked into chaotically distributed flat pebbles (text-fig. 1E), and higher above into limestone with ooids. The next fossiliferous stratum is about 6 m



TEXT-FIGURE 4
Stratigraphic distribution of relatively well known Shumardiidae species and probable location of the new finding from the Lung Cu section. Generic names are given only for their type species. Crucial evolutionary novelties (apomorphies) are indicated in grey.



TEXT-FIGURE 5
Conodonts from the brachiopod coquina in the Lung Cu section.

A–D *Cordylodus angulatus*, P_1 ZPAL V.47/80 (A) and S series ZPAL V.47/74, 72 and 79 (B–D) elements.

E *Semiacontiodus* sp. asymmetric element ZPAL V.47/71.

above, and is composed of unidentifiable fragments of orthoid brachiopod shells and broken polymerid trilobite exoskeletons. A 10 kg sample yielded only five conodont elements. They are characteristic enough to enable testing the trilobite-based dating.

CONODONT TEST OF TRILOBITE DATING

Of the five elements found in the brachiopod coquina at the Lung Cu section, one represents an asymmetric coniform element characteristic of an apparatus of the *Teridontus* lineage. Such elements evolved slowly in the latest Cambrian and early Ordovician and are of limited use biostratigraphically. The remaining denticulate elements represent *Cordylodus*, the fast-evolving conodont widely used in biostratigraphy of the latest Cambrian and the Tremadocian.

The probable ancestor of *Cordylodus* is probably *Eoconodontus notchpeakensis* with all elements of the apparatus coniform but of shape similar to denticulated elements of geologically younger members of the lineage (e.g., Dubinina 2001). In the late Cambrian populations of *Cordylodus andresi* from the Baltic region (Kaljo et al. 1986; Viira et al. 1987), juvenile specimens lack denticulation, which develops in later stages of the organogeny.

Cordylodus primitivus from Newfoundland (Bagnoli et al. 1987) was proposed to be the earliest member of the lineage but the sample, in which the type specimen of the species was chosen also yielded the type specimen of the much more advanced *C. caboti*. The name *C. caboti* was subsequently used by Nicoll (1991, fig. 3) for populations transitional in age and morphology between *C. proavus* and *C. prolindstromi*, that is at relatively late stage of the evolution of *Cordylodus*. He also considered the possibility that *C. caboti* is transitional between *C. proavus* and *C. angulatus*, as suggested by morphology of the base of the P element. Thus, either the original sample of Bagnoli et al. (1987) contains mixed fossil assemblages reworked from strata of different ages or *C. caboti* as interpreted by Nicoll (1991) is a different chronospecies. Elements assigned to *C. caboti* by Bagnoli et al. (1987) may represent other parts of the apparatus of *C. primitivus*.

The geographic distribution of *Cordylodus andresi* was wide enough to allow use of its first appearance to define the base of the Ibexian Series in North America (Miller et al. 2001, 2006). In Sweden (Öland) it occurs in the latest Cambrian *Acerocare* Zone (Andres 1988). In its type locality, Vihula, there is a continuity between *C. andresi* and its successor *C. proavus*. The apparatus composition of *Cordylodus proavus* is known owing to a six element cluster found by Andres (1981, 1988). During the course of evolution, the basal cavity of its elements became shallower and the cusp more robust (Viira et al. 1987). In another section, Naziya, a transformation of *C. proavus* into even more advanced *C. lindstromi* has been documented by bed-by-bed sampling (Viira et al. 1987). A cluster of three elements of *C. lindstromi* in presumably original disposition, parallel to each other and with the tips of denticles of other elements in opposing orientation was studied by Smith et al. (2005). In this segment of the lineage, the basal cavity gradually developed an additional pit below the first denticle. The same succession was observed by Nicoll (1991) in the Ninmaroo Formation in Queensland, but there are gaps in the distribution of the lineage below and above the transitional form named *C. prolindstromi*. The gap may be preservational but a possibility remains that the Baltic region (probably also the North American Great Basin and Hunan province of China; Miller 1980; Ross et al. 1997; Miller et al. 2003, 2015; Dong et al. 2004) was within the area of phyletic evolution of the lineage, whereas Australia was invaded by successive populations representing various stages of the lineage's evolution. This means that two coeval but initially allopatric lineages of *Cordylodus* existed that time.

Although a dual-tipped basal cavity is not unique to *Cordylodus lindstromi*, its distinction from the partly coeval and commonly sympatric *C. angulatus* is apparent, with no transitions. Also *Cordylodus angulatus* lineage has its ancestry in *C. proavus*, but there seems to be no continuity between these chronospecies in the Baltic area. Such an intermediate has been identified by Nicoll (1990) in Queensland as his *C.* sp. nov. A. Its P series elements have an incipient convexity at the base. In typical *C. angulatus*, this changes into the 'Phrygian cap' shape (Nicoll 1990). Such an element has been found in the Lung Cu section (text-fig. 5A) associated with two others that may fit into one of the asymmetric S series elements recognized by Nicoll (1990). Although the conodont oral apparatus composition may be very complex (e.g., Dzik 2015) in the case of *Cordylodus*, knowledge of the morphology of any P and S elements is sufficient to determine species. Andres (1981, fig. 20) suggested that the apparatus of *Cordylodus* consisted of seven pairs of elements, the elements of largest size being located in its middle and except for the marginal locations they are of similar shape.

The conodonts establish that the brachiopod coquina is of late early Tremadocian age (Miller 2013; Saltzman et al. 2014) and the bed with shumardid trilobites is older. Additional support for such dating is offered by the contents of sample SS 1080, taken about 30 m above the coquina. It has yielded single specimens of *Cordylodus angulatus, Semiacontiodus* sp. and *Iapetognathus sprakersi* (Nicoll et al. 1999), but also *Chosonodina herfurthi*, the very characteristic and widespread species typically associated with *C. angulatus* (Chen and Gong 1986; Nicoll 1991; Lehnert et al. 2005; Zhen et al. 2014). *Chosonodina* is perhaps an Ordovician paraconodont derived from *Westergaardodina*, with *C. tridentata* being a morphologically (but not stratigraphically) transitional form (Chen and Gong 1986). *Chosonodina* originated at an unknown time and place (Lehnert et al. 2005) and its first appearance is not necessarily synchronous across its geographic range. All together, this fossil assemblage suggests a mid-Tremadocian age. The age of the bed with shumardiid trilobites can be assumed as older than, or within the range of, the *C. angulatus* Zone. The *Cordylodus* lineage was present in the area much earlier, as shown by sample SS 14/2 from the nearby Chang Pung section, located 16.5 km southeast of the Lung Cu section (text-fig. 1A). The source bed is located immediately below the discordantly overlying Devonian sandstone. The fossil assemblage includes only highly variable *Cordylodus* elements with variable depths of the basal cavity and relatively late ontogenetically development of denticles in S series elements. Tectonic deformation of the elements makes comparison difficult, but the population represented by the sample seems transitional between *C. andresi* and *C. proavus*. This dates the stratum as close to the base of the Ordovician.

CONCLUSIONS

Incompleteness of the fossil record influences precision of palaeontologically-based age determination, but the way of reasoning remains the same, irrespective of sampling density and group of fossil organisms used. Implicitly, an evolutionary succession of forms is the reference standard, to which a new finding is compared. In case of the Lung Cu section samples, the dating of the fossil assemblage with *Iapetognathus* and *Chosonodina* can be interpreted biostratigraphically using homotaxy as the mode of inference. No species in the assemblage has a precisely determined time of origin, but one may consider their co-occurrence as resulting from geographically widespread change of ecological conditions, which controlled their distribution.

The reasoning used to infer geological age of the shumardiid trilobite from the bed with flat concretions is more explicitly connected with evolution. Probably the most reliable age constraint can be provided by data from the *Cordylodus* conodonts. Dense sampling of the continuous succession of the *C. andresi* to *C. lindstromi* lineage in the Baltic region and the almost continuous succession of the *C. proavus* to *C. angulatus* lineage in Australia has enabled restoration of their evolution on (almost) a population level. This has made possible to specify the age of strata containing fossils of these conodont chronospecies with a high degree of certainty. Dating based on evolutionary grade is unavoidably less precise than that referring to environmental changes because the rate of morphological evolution observed in rocks is generally low. Nevertheless, the unrepeatability of evolution makes this way of reasoning much more reliable than that based on repeatable and mostly diachroneous migrations of organisms controlled by ecological factors. Only after crude (but reliable) evolutionary evidence is available can dating be more precise by supplementing it with ecologically controlled faunal, magnetostratigraphic or geochemical data.

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