Siphonodella leiosa (Conodonta), a new unornamented species from the Tournaisian (lower Carboniferous) of Puech de la Suque (Montagne Noire, France)

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Abstract

A new conodont species, *Siphonodella leiosi*, is described from the lower Carboniferous pelagic limestones of the Montagne Noire (France), deposited on North Gondwana in outer platform environment. Specimens were obtained from one level dated to the *Siphonodella jii* conodont Zone. The major difference from other siphonodellid conodonts known in this area is that the elements of this new species have a practically entirely smooth and unornamented platform, apart from the development of one or two low rostral ridge-like nodes. Similar morphologies were generally observed in shallow marine deposits of the same time frame from China, Russia and East and Central European areas. The new discovery reinforces the idea that ornamentation of siphonodellids is not only related to bathymetry, but that temperature could play an important role in the diversification and radiation of unornamented species during the *Siphonodella jii* conodont Zone.

Keywords

Carboniferous, conodonts, *Siphonodella*, Montagne Noire

1. Introduction

The study of the Puech de la Suque pelagic section in the Montagne Noire (France) for high resolution stratigraphy through the Devonian/Carboniferous boundary resulted in an abundant and diverse conodont fauna collection (Feist et al., 2020). Conodonts are marine jawless vertebrates that lived from the late Cambrian to the Late Triassic. They are mainly known in the fossil record by their small teeth-like feeding structures called conodont elements. These elements are widely recognized as valuable tools for biostratigraphy, due to their abundance, high evolutionary rate, and good spatial and temporal record over long periods of time (Sweet, 1988).

Among conodonts, *Siphonodella* species are key stratigraphic markers to date the base of the Carboniferous. The first appearance datum of *Siphonodella sulcata* (Huddle) defines the base of the Carboniferous (Paproth et al., 1991). Other species of *Siphonodella* are used as index fossils for Tournaisian (lower Carboniferous) conodont zonations (Sandberg et al., 1978; Jii, 1985; Kaiser et al., 2009; Becker et al., 2016; Corradini et al., 2017; Hogancamp et al., 2019).

Siphonodella platform elements are usually ornamented, meaning that they bear nodes and ridges on the oral surface. The general shape of the platform and ornamentation are criteria used for taxonomy. *Siphonodella* is commonly associated with offshore open-marine environments with mesopelagic habitat (e.g. Austin, 1976; Ziegler & Sandberg, 1984; Savoy & Harris, 1993; Kalvoda et al., 1999; Kaiser et al., 2008). The ornamented *Siphonodella*: *Siphonodella bransoni* Ji*, Si. carinthiaca* Schönlaub*, Si. cooperi* Hass*, Si. crenulata* Cooper, *Si. duplicata* (Branson & Mehl)*, Si. isosticha* Cooper, *Si. jii* Becker et al.*, Si lobata* (Branson & Mehl), *Si. obsoleta* Hass*, Si. praesulcata* Sandberg*, Si. quadruplicata* (Branson & Mehl), *Si. sandbergi* Klapper and *Si. sulcata* (Huddle) are considered pelagic species.

In Eastern and Central Europe, Russia, and China, species of *Siphonodella* that have a smooth oral surface without ornamentation have been described. These include: *Siphonodella belkai* Dzik*, Si. bella* Kononova & Migdisova*, Si. dasaibaensis* Ji, *Si. eurylobata* Ji, *Si. homosimplex* Ji & Ziegler*, Si. kalvodai* Kaiser, Kumpan & Cigler, *Si. levis* Ni*, Si. puchovki* Zhuravlev, *Si. quasinuda* Gagiev Kononova & Pazuhin, *Si. simplex* Ji, *Si. sinensis* Ji and *Si. uralica* Zhuravlev (e.g. Coen & Groessens, 1996; Dzik, 1997; Gagiev *et al.,* 1987; Ji, 1987; Ji &

Ziegler, 1992; Kaiser et al., 2017; Kononova & Lipnjagov, 1976; Li et al., 2014; Lipnjagov, 1979; Malec, 2014; Matyja, 1976; Qie et al., 2014; Qin et al., 1988; Zhuravlev & Plotitsyn, 2017; Zhuralev, 2019). They are found in Tournaisian neritic carbonate platform and slope facies, especially in the eastern and northern part of the Paleotethys realm. A "shallow-water" conodont zonation utilizing unornamented siphonodellids was proposed (Ji, 1987; 1988; Qie et al., 2014). In China (Ji, 1987; 1989), as well as in Russia (Zhuravlev, 2017), ornamented siphonodellids co-occur with unornamented species, allowing the correlation of "deep" and "shallow" water zonations.

Recently, Kaiser et al. (2017) found unornamented species (*Si. belkai* and *Si. kalvodai*) from the *jii* Zone in western part of Paleotethys. *Siphonodella belkai* was described from Kowala, Poland (Dzik, 1997 ; Malec, 2014). Kaiser et al. (2017) concluded that unornamented siphonodellids were able to invade the western part of the Paleotethys, but not north Gondwanan areas, due to the presence of the large Paleotethys ocean, nor eastern Laurussia, probably due to a terrestrial barrier.

One layer of strata in the *Siphonodella jii* Zone from the north Gondwana area in the Puech de la Suque section (Montagne Noire, France) yielded siphonodellid specimens that have an outline close to ornamented siphonodellids from this age, but differed in having a smooth and unornamented platform. This occurrence is coincident with the increased diversity within the genus *Siphonodella* observed at a global scale during the *Si. jii* Zone. This paper describes a new unornamented *Siphonodella* species, as well as the ecological and environmental significance of this taxon.

2. Geological setting

The Puech de la Suque section is located on the southeastern slope of the Puech de la Suque hill, near St Nazaire de Ladarez in the Montagne Noire (France) 43°29'59.7"N 3°05'54.8"E (Fig. 1(A)). This outcrop is tectonically inverted (Fig. 1(B)). The end-Famennian shales deposited during the regressive event of the Hangenberg Crisis are overlain by the Tournaisian succession recording transgressive trend from middle platform to basinal settings (Girard, 1994; Feist et al., 2020). The shales are superseded by the reappearance of carbonate sedimentation with 2m of gray-yellowish, nodular, dm-thick bedded mudstone to wackestone. These limestones contain ostracods (Lethiers & Feist, 1991) and conodonts

(Boyer et al., 1968; Girard, 1994, Kaiser, 2005; Feist et al., 2020), and are are topped by well-bedded thin intercalations of cherts.

3. Material

New samples from the Puech de la Suque section yielded unornamented siphonodellid specimens from bed PS20, exclusively, located 1.2 meter above the base of the Carboniferous (Girard, 1994; Feist et al., 2020). The conodonts were extracted from this level in the laboratory of the University of Montpellier (France). Two kilograms of rock were dissolved using formic acid (10%) and then rinsed through 100µm and 1mm sieves. Conodonts were removed from the insoluble residue using a binocular microscope (Nikon SM8). Among the fifty *Siphonodella* specimens, nine were unornamented. The nine specimens were imaged using an X-ray microtomograph (µCT) Phoenix nanotomeS on the AniRA-Immos platform of the SFR Biosciences (UMS 3444, ENS Lyon) at a cubic voxel resolution of 1 µm. All specimens, holotypes and paratypes (UM PSQ 1 to UM PSQ 9), were housed in the collections of the University of Montpellier, and their 3D reconstructions (UM PSQ 1 to UM PSQ 9) were deposited in MorphoMuseum (Souquet et al., 2020).

4. Systematic Paleontology

Phylum Chordata Bateson, 1886

Class Conodonta Pander, 1856

Order Ozarkodinida Dzik, 1976

Family Elictognathidae Austin & Rhodes, 1981

Genus *Siphonodella* Branson & Mehl, 1944

Type species: *Siphonognathus duplicata* Branson & Mehl, 1934

Siphonodella leiosi sp. nov.

Figure 2

HOLOTYPE: dextral P1 element (UM PSQ 2), figured in Fig. 2(B).

PARATYPES: Figured P1 elements (UM PSQ 1, 3 to 9).

STRATUM TYPICUM: Bed of sample PS20.

TYPE LOCALITY: Puech de la Suque section, Montagne Noire, France.

DERIVATIO NOMINIS: From the Greek leios: slick, smooth

OCCURRENCE: *Siphonodella jii* Zone (lower Tournaisian).

MATERIAL: 9 specimens from Puech de la Suque section.

DIAGNOSIS: A species of *Siphonodella* whose P1 element is characterized by an asymmetric unornamented platform with a unilateral rostral ridge composed of nodes on the inner side. The lower side bears a wide pseudokeel.

DESCRIPTION: The P1 element of *Siphonodella leiosi* sp. nov. is characterized by an asymmetric smooth platform arched downward with apex of arch at position of the pit. Inner platform lanceolate and outer platform ovate. The short rostral ridge on the inner platform is composed of 3 to 5 discrete nodes. The anterior part of outer platform is strongly reduced. The short free blade bears partially fused and laterally flattened sharp denticles. Low incurved carina with nodes on posterior part of the platform. The aboral side of the element (lower view) is typical of the *Siphonodella* genus. It presents a wide pseudokeel which narrows anteriorly to the pit, the latter being placed slightly more posteriorly than the middle of the element.

REMARKS: The species differs from other taxa of *Siphonodella* by the lack of ornementation, the shape of the very large and unornamented platform, and presence of the lateral rostrum ridge composed of nodes. Very reduced nodes may be developed on some specimens on the outer platform. This new species shows similar outline compared to ornamented species from Montagne Noire, but does not have ornamentation on the platform excepting one or two rostral ridge(s) that converge toward the carina. *Siphonodella leiosi* sp. nov. differs from unornamented species from the eastern part of the Paleotethys by the larger rostrum with well-differentiated nodes which converge towards the carina. Kalvoda et al. (2015, fig. 5(3)) illustrated an element from the *jii* Zone of Lesní lom, Moravia, that is similar to our element illustrated in Fig. 2(I), being slightly different by the more strongly developed rostral ridges.

158 This form may enter in the variability of *Si. leiosi*. The occurrence of the species in Moravia is
159 confirmed by the recovery of another specimen from the same section and biozone (T.
160 Kumpan, pers.com).
161
162
163 **5. Discussion**
164
165 Due to their global geographical distribution most of the species of the genus
166 *Siphonodella* are used for stratigraphic subdivision of the uppermost Famennian and lower
167 Tournaisian (e.g. Sandberg et al., 1978). The ornamented taxa are interpreted as inhabitants
168 of offshore environments. Distinctive features include platform outline, development of a
169 keel, nature of the rostrum and rostral ridges, as well as the nature of nodes and ridges on
170 the inner and outer platform.
171 At the beginning of the Tournaisian, unornamented *Siphonodella* species are present
172 on the eastern border of the Paleotethys. Two regions of endemism are recognized: South
173 China and western Asia (Tajikistan, Kazakhstan, and Urals) (Figure 3(A)).
174 From the *jii* Zone, around 1.5 My after the Devonian/Carboniferous boundary (Davydov
175 et al. 2012) an important radiation of ornamented siphonodellids (Sandberg et al., 1978)
176 occurs worldwide (Kaiser et al., 2017 for a review). A diversification of endemic
177 unornamented species was also observed in China and Russia (Ji, 1985 ; Zhuravlev, 2017). At
178 the same time, unornamented species appeared on the western border of the Paleotethys
179 realm for the first time with the recognition of *Si. belkai*, *Si. kalvodai,* and *Si. leiosi* sp. nov.
180 (Figure 3(B)).
181 The *jii* Zone is a period of radiation of ornamented siphonodellids with the first
182 occurrence of the cosmopolitan species *Si. jii*, *Si. cooperi*, *Si. obsoleta* and *Si. carinthiaca*. In
183 China and Russia (s. l.), the unornamented species also radiated and diversified, with *Si.*
184 *belkai* and *Si. dasaibaensis* in China (Ji & Ziegler, 1992., Li et al., 2014); and *Si. semichatovae*
185 and *Si. ludmilae* in Russia (Zhuralev, 2017).
186 Based on the stratigraphic distribution of taxa in different regions it is possible to
187 suppose the migration route of some species along the Palaeothetys: *Si. belkai* (Kaiser et al.,
188 2017), is known in China and is present from the base of the *jii* Zone in western and eastern

parts of the Paleotethys, and becomes abundant in eastern Europe only in the upper part of the *jii* Zone (Kaiser et al., 2017).

The Devonian / Carboniferous boundary coincides with a major regressive phase followed by a deepening during the Tournaisian (Girard, 1994; Haq & Schutter, 2008). The migration and dispersion of smooth species could be synchronous with transgressive periods. This scenario was suggested by Narkiewicz & Sculc (2004) and Kaiser et al. (2017) to explain dispersion of conodont faunas throughout the Tethys.

The *Siphonodella jii* Zone is also characterized by the first occurrence of two new species on the western part of the Paleotethys: *Si. leiosi* (this study), and *Si. kalvodai*. Kaiser et al. (2017, p. 17) noted that *Si. kalvodai* resembles *Si. belkai* (M1 and M2), « but differs in having a crenulated outer margin and by rostral ridges only on the anterior part of the platform ». It cannot be excluded that *Si. kalvodai* evolved from *Si. belkai* or from the same ancestor on western part of Paleotethys when local environmental conditions became favorable.

The history of *Siphonodella leiosi* is different as it does not resemble any other described species (except minor similarities in the outline with *Si. duplicata* ?), nor from east Paleotethys. As smooth species are supposed to prefer shallow-waters, the radiation and development of unornamented species all around the Paleotethys could be due to a global regression. However, this contradicts the scenario that suggests a transgressive phase allowing the migration of *Si. belkai* from the eastern part of the Paleotethys to the western part. Furthermore, biofacies and sedimentological analyses of sections in Montagne Noire (Girard, 1994; Feist et al., 2020) confirm a deepening through the basal Tournaisian after the major regression associated with Hangenberg Crisis just before the Devonian/Carboniferous boundary.

From the Devonian/Carboniferous boundary to the *jii* Zone, there is an increase in temperature of approximately 2-3°C, which remained stable thereafter (Buggisch et al., 2008). The diversification of unornamented siphonodellids was coincident with the warmest time. Shallow seas must be warmer than deep seas, and unornamented species have an equatorial repartition in the beginning of the Carboniferous. Associated, or not, with depth, the temperature could have played a role in development and selection of smooth siphonodellids.

Conclusions

A smooth siphonodellid was found in North Gondwana in the Montagne Noire (France) for the first time. This new species *Siphonodella leiosi* is characterized by an asymmetric smooth platform, a short rostral ridge on the inner platform composed of 3 to 5 discrete nodes, an anterior part of outer platform strongly reduced. The radiation and development of unornamented species all around the Paleotethys could be due to global changes in temperatures, associated, or not, to change in water depth.

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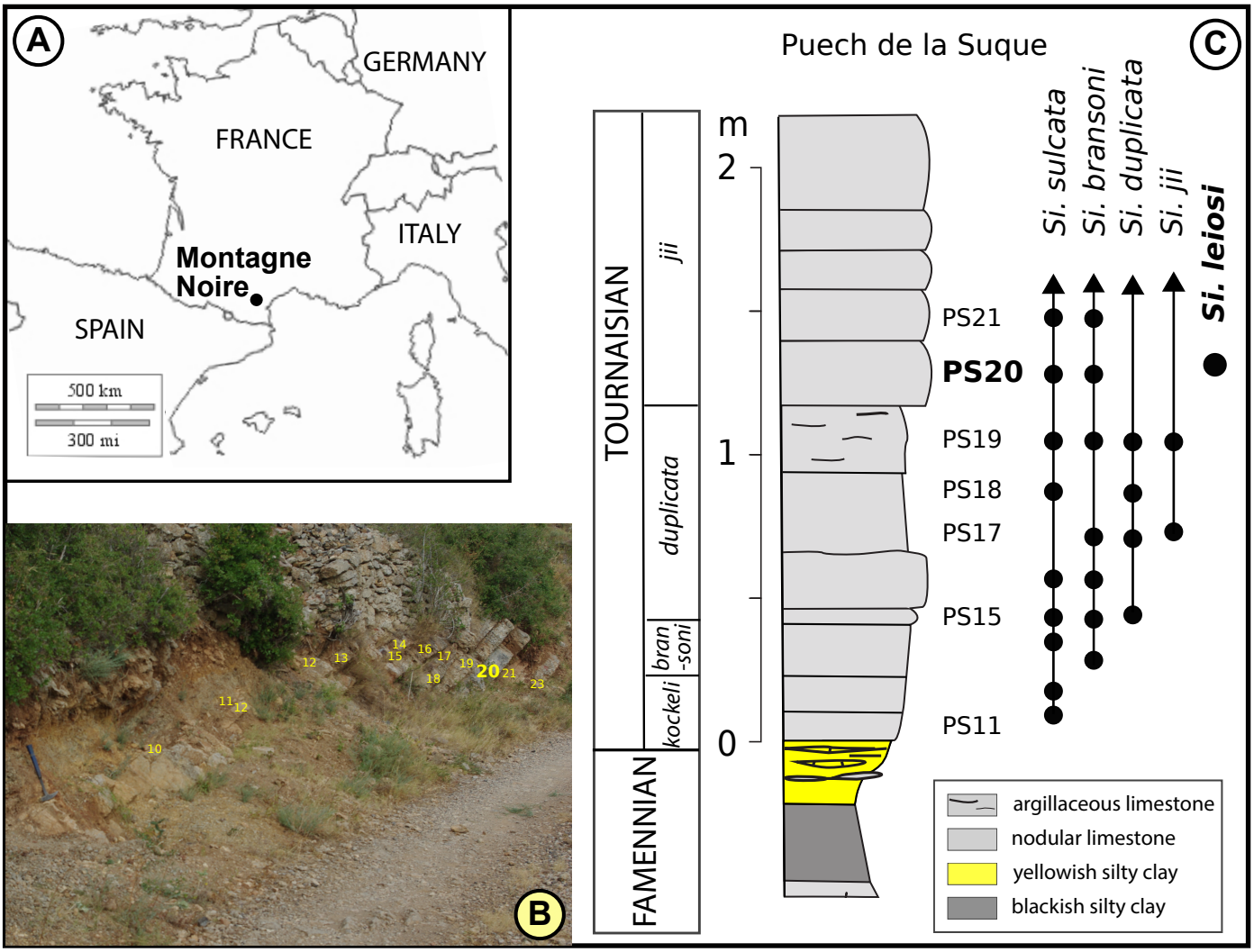
Figure captions

Figure 1: A. Location of the studied area, the Montagne Noire (France). B. View of the inverted beds exposed in Puech de la Suque. C. Log of the lithological succession in the Puech de la Suque (PS) with occurrence of the species of *Siphonodella*. Conodont Zones after Corradini et al. (2017).

Figure 2: *Siphonodella leiosi* new species. From right to left: upper, lower and lateral views of P1 element (UM PSQ 1 to 9),. A: Paratype UM PSQ 1; B: Holotype UM PSQ 2; C: Paratype UM PSQ 3; D: UM PSQ 4; E: UM PSQ 5; F: UM PSQ 6; G: UM PSQ 7; H: UM PSQ 8; I: UM PSQ 9. Scale bar: 500 µm.

Figure 3: Tournaisian paleogeographic maps with the main currents and their directions (Scotese, 2016) showing the paleogeographic distribution of unornamented siphonodellids (A) from the *Protognathodus kockeli* Zone to the *Si. duplicata* Zone), and (B) during the *Siphonodella jii* Zone (Corradini et al., 2017). In bold, species not present before the *Si. jii* Zone. Illustrations of the siphonodellids from Ji & Ziegler (1992), Kaiser et al. (2017); Zhuravlev & Plotitsyn (2017), and this study. Rep. : Republic, *Pr.*: *Protognathodus*, *Si.*: *Siphonodella*.

Figure 1


A
GERMANY
FRANCE
ITALY
Montagne Noire
SPAIN
500 km
300 mi
B
C
Puech de la Suque
TOURNAISIAN
FAMENNIAN
jii
duplicata
bran -soni
kockeli
m
2
1
0
PS21
PS20
PS19
PS18
PS17
PS15
PS11
Si. sulcata
Si. bransoni
Si. duplicata
Si. jii
Si. leiosi
argillaceous limestone
nodular limestone
yellowish silty clay
blackish silty clay

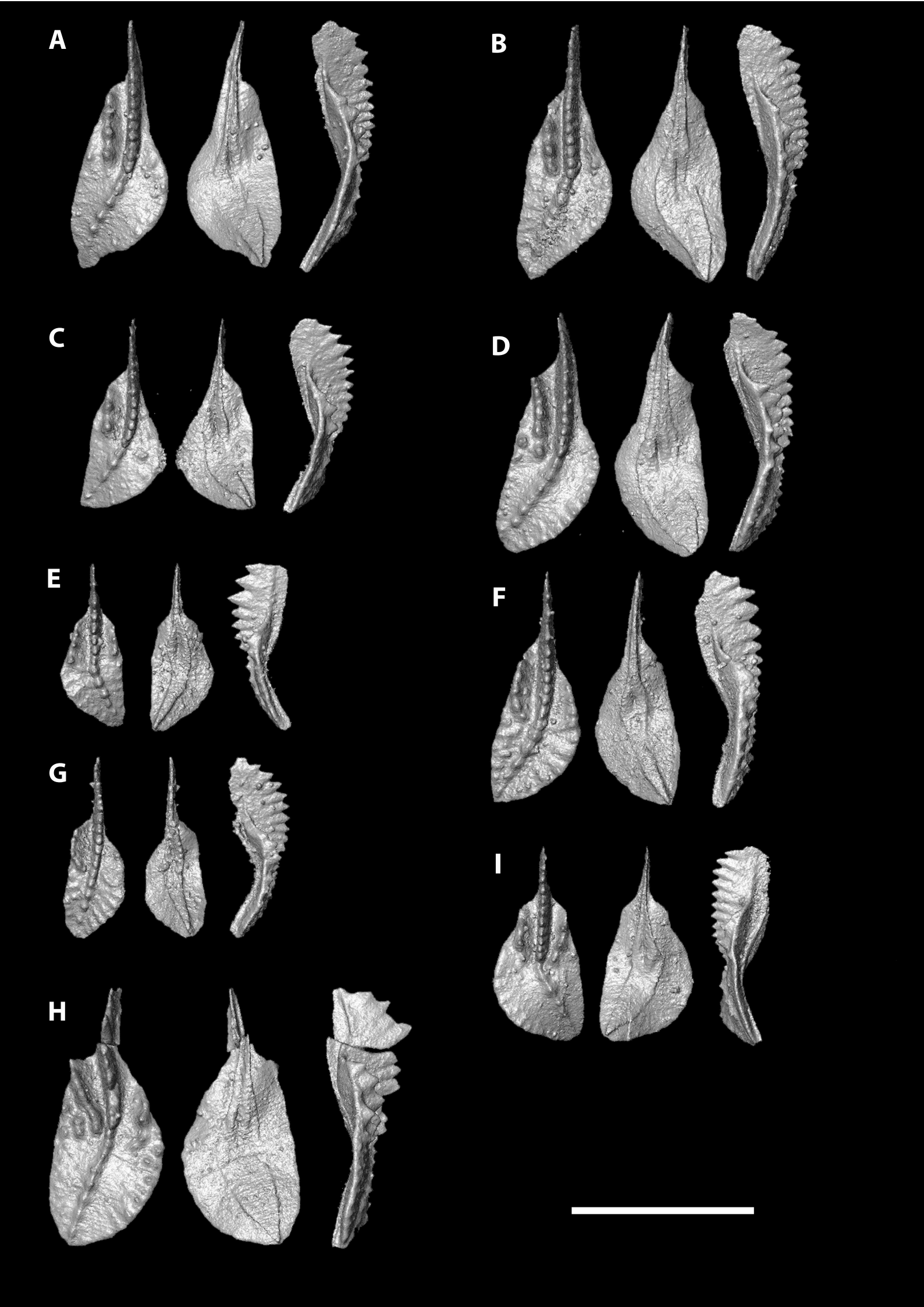
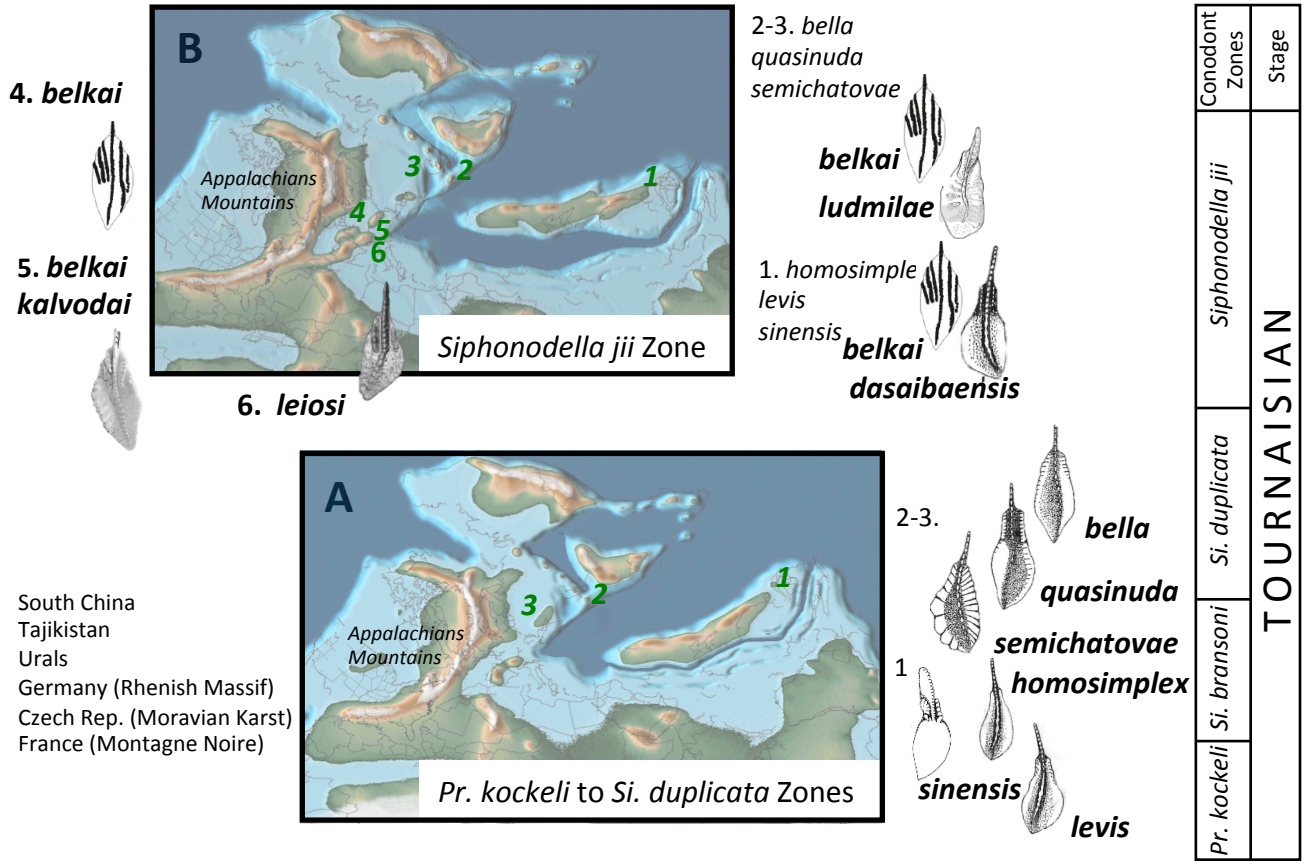

A
B
C
D
E
F
G
I
H

Figure 3



1. South China
2. Tajikistan
3. Urals
4. Germany (Rhenish Massif)
5. Czech Rep. (Moravian Karst)
6. France (Montagne Noire)