

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

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Siphonodella leiosi (Conodonta), a new unornamented species from the 1 Tournaisian (lower Carboniferous) of Puech de la Sugue (Montagne Noire, 2 3 France) 4 Louise Souquet<sup>a, b</sup>, Carlo Corradini<sup>c</sup> and Catherine Girard<sup>d, \*</sup> 5 6 7 <sup>a</sup> Centre de Recherche en Paléontologie - Paris, UMR CNRS 7207, CP 38, Muséum National d'Histoire Naturelle, 75005 Paris, France 8 9 <sup>b</sup> Mécanismes Adaptatifs et Evolution, UMR CNRS 7179, Bâtiment Anatomie Comparée, CP 55, Muséum National d'Histoire Naturelle, 75005 Paris, France 10 <sup>c</sup> Dipartimento di Matematica e Geoscienze, Università di Trieste, via Weiss 2, 34128 Trieste, 11 12 Italy 13 <sup>d</sup> ISEM, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France. (\* corresponding author: 14 Catherine.Girard@umontpellier.fr)

15

#### 16 Abstract

A new conodont species, Siphonodella leiosi, is described from the lower Carboniferous 17 pelagic limestones of the Montagne Noire (France), deposited on North Gondwana in outer 18 platform environment. Specimens were obtained from one level dated to the Siphonodella jii 19 conodont Zone. The major difference from other siphonodellid conodonts known in this area 20 21 is that the elements of this new species have a practically entirely smooth and 22 unornamented platform, apart from the development of one or two low rostral ridge-like 23 nodes. Similar morphologies were generally observed in shallow marine deposits of the 24 same time frame from China, Russia and East and Central European areas. The new 25 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 26 radiation of unornamented species during the Siphonodella jii conodont Zone. 27

28

#### 29 Keywords

- 30 Carboniferous, conodonts, Siphonodella, Montagne Noire
- 31

32 **1. Introduction** 

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The study of the Puech de la Suque pelagic section in the Montagne Noire (France) 34 35 for high resolution stratigraphy through the Devonian/Carboniferous boundary resulted in 36 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 37 38 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 39 40 their abundance, high evolutionary rate, and good spatial and temporal record over long periods of time (Sweet, 1988). 41

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).

48 Siphonodella platform elements are usually ornamented, meaning that they bear 49 nodes and ridges on the oral surface. The general shape of the platform and ornamentation 50 are criteria used for taxonomy. Siphonodella is commonly associated with offshore open-51 marine environments with mesopelagic habitat (e.g. Austin, 1976; Ziegler & Sandberg, 1984; 52 Savoy & Harris, 1993; Kalvoda et al., 1999; Kaiser et al., 2008). The ornamented 53 Siphonodella: Siphonodella bransoni Ji, Si. carinthiaca Schönlaub, Si. cooperi Hass, Si. 54 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 55 (Branson & Mehl), Si. sandbergi Klapper and Si. sulcata (Huddle) are considered pelagic 56 57 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 & 64 Ziegler, 1992; Kaiser et al., 2017; Kononova & Lipnjagov, 1976; Li et al., 2014; Lipnjagov, 65 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 66 facies, especially in the eastern and northern part of the Paleotethys realm. A "shallow-67 water" conodont zonation utilizing unornamented siphonodellids was proposed (Ji, 1987; 68 1988; Qie et al., 2014). In China (Ji, 1987; 1989), as well as in Russia (Zhuravlev, 2017), 69 70 ornamented siphonodellids co-occur with unornamented species, allowing the correlation of "deep" and "shallow" water zonations. 71

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.

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#### 86 2. Geological setting

The Puech de la Suque section is located on the southeastern slope of the Puech de la 87 88 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 89 shales deposited during the regressive event of the Hangenberg Crisis are overlain by the 90 Tournaisian succession recording transgressive trend from middle platform to basinal 91 92 settings (Girard, 1994; Feist et al., 2020). The shales are superseded by the reappearance of 93 carbonate sedimentation with 2m of gray-yellowish, nodular, dm-thick bedded mudstone to wackestone. These limestones contain ostracods (Lethiers & Feist, 1991) and conodonts 94

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

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#### 98 **3. Material**

New samples from the Puech de la Sugue section yielded unornamented 99 100 siphonodellid specimens from bed PS20, exclusively, located 1.2 meter above the base of the 101 Carboniferous (Girard, 1994; Feist et al., 2020). The conodonts were extracted from this level 102 in the laboratory of the University of Montpellier (France). Two kilograms of rock were 103 dissolved using formic acid (10%) and then rinsed through 100µm and 1mm sieves. 104 Conodonts were removed from the insoluble residue using a binocular microscope (Nikon 105 SM8). Among the fifty Siphonodella specimens, nine were unornamented. The nine specimens were imaged using an X-ray microtomograph (µCT) Phoenix nanotomeS on the 106 107 AniRA-Immos platform of the SFR Biosciences (UMS 3444, ENS Lyon) at a cubic voxel 108 resolution of 1  $\mu$ m. All specimens, holotypes and paratypes (UM PSQ 1 to UM PSQ 9), were 109 housed in the collections of the University of Montpellier, and their 3D reconstructions (UM 110 PSQ 1 to UM PSQ 9) were deposited in MorphoMuseum (Souquet et al., 2020).

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#### 112 4. Systematic Paleontology

- 113 Phylum Chordata Bateson, 1886
- 114 Class Conodonta Pander, 1856
- 115 Order Ozarkodinida Dzik, 1976
- 116 Family Elictognathidae Austin & Rhodes, 1981
- 117 Genus Siphonodella Branson & Mehl, 1944
- 118 **Type species:** Siphonognathus duplicata Branson & Mehl, 1934
- 119
- 120 Siphonodella leiosi sp. nov.
- 121 Figure 2
- 122 **HOLOTYPE:** dextral P1 element (UM PSQ 2), figured in Fig. 2(B).
- 123 **PARATYPES:** Figured P1 elements (UM PSQ 1, 3 to 9).
- 124 **STRATUM TYPICUM:** Bed of sample PS20.
- 125

- 126 **TYPE LOCALITY:** Puech de la Suque section, Montagne Noire, France.
- 127

128 **DERIVATIO NOMINIS:** From the Greek leios: slick, smooth

129

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

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132 **MATERIAL:** 9 specimens from Puech de la Suque section.

133

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.

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138 **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. 139 Inner platform lanceolate and outer platform ovate. The short rostral ridge on the inner 140 141 platform is composed of 3 to 5 discrete nodes. The anterior part of outer platform is strongly 142 reduced. The short free blade bears partially fused and laterally flattened sharp denticles. 143 Low incurved carina with nodes on posterior part of the platform. The aboral side of the 144 element (lower view) is typical of the Siphonodella genus. It presents a wide pseudokeel 145 which narrows anteriorly to the pit, the latter being placed slightly more posteriorly than the 146 middle of the element.

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148 **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 149 150 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 151 from Montagne Noire, but does not have ornamentation on the platform excepting one or 152 two rostral ridge(s) that converge toward the carina. Siphonodella leiosi sp. nov. differs from 153 154 unornamented species from the eastern part of the Paleotethys by the larger rostrum with 155 well-differentiated nodes which converge towards the carina. Kalvoda et al. (2015, fig. 5(3)) 156 illustrated an element from the jii Zone of Lesní lom, Moravia, that is similar to our element 157 illustrated in Fig. 2(I), being slightly different by the more strongly developed rostral ridges. This form may enter in the variability of *Si. leiosi*. The occurrence of the species in Moravia is confirmed by the recovery of another specimen from the same section and biozone (T. Kumpan, pers.com).

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#### 163 **5. Discussion**

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Due to their global geographical distribution most of the species of the genus *Siphonodella* are used for stratigraphic subdivision of the uppermost Famennian and lower Tournaisian (e.g. Sandberg et al., 1978). The ornamented taxa are interpreted as inhabitants of offshore environments. Distinctive features include platform outline, development of a keel, nature of the rostrum and rostral ridges, as well as the nature of nodes and ridges on the inner and outer platform.

At the beginning of the Tournaisian, unornamented *Siphonodella* species are present on the eastern border of the Paleotethys. Two regions of endemism are recognized: South China and western Asia (Tajikistan, Kazakhstan, and Urals) (Figure 3(A)).

From the *jii* Zone, around 1.5 My after the Devonian/Carboniferous boundary (Davydov et al. 2012) an important radiation of ornamented siphonodellids (Sandberg et al., 1978) occurs worldwide (Kaiser et al., 2017 for a review). A diversification of endemic unornamented species was also observed in China and Russia (Ji, 1985 ; Zhuravlev, 2017). At the same time, unornamented species appeared on the western border of the Paleotethys realm for the first time with the recognition of *Si. belkai, Si. kalvodai,* and *Si. leiosi* sp. nov. (Figure 3(B)).

The *jii* Zone is a period of radiation of ornamented siphonodellids with the first occurrence of the cosmopolitan species *Si. jii, Si. cooperi, Si. obsoleta* and *Si. carinthiaca*. In China and Russia (s. l.), the unornamented species also radiated and diversified, with *Si. belkai* and *Si. dasaibaensis* in China (Ji & Ziegler, 1992., Li et al., 2014); and *Si. semichatovae* and *Si. ludmilae* in Russia (Zhuralev, 2017).

Based on the stratigraphic distribution of taxa in different regions it is possible to suppose the migration route of some species along the Palaeothetys: *Si. belkai* (Kaiser et al., 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.

203 The history of Siphonodella leiosi is different as it does not resemble any other 204 described species (except minor similarities in the outline with Si. duplicata ?), nor from east 205 Paleotethys. As smooth species are supposed to prefer shallow-waters, the radiation and 206 development of unornamented species all around the Paleotethys could be due to a global 207 regression. However, this contradicts the scenario that suggests a transgressive phase 208 allowing the migration of *Si. belkai* from the eastern part of the Paleotethys to the western 209 part. Furthermore, biofacies and sedimentological analyses of sections in Montagne Noire 210 (Girard, 1994; Feist et al., 2020) confirm a deepening through the basal Tournaisian after the 211 major regression associated with Hangenberg Crisis just before the Devonian/Carboniferous boundary. 212

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.

220

#### 221 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

225 anterior part of outer platform strongly reduced. The radiation and development of 226 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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#### 358 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).

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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.

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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*.





![](_page_14_Figure_1.jpeg)