

## THE CONODONT GENUS *TERIDONTUS* (MILLER, 1980) FROM THE EARLY ORDOVICIAN OF MONTAGNE NOIRE, FRANCE

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### INTRODUCTION

THE CONODONT genus *Teridontus* was introduced in 1980 by Miller and was based on the Late Cambrian species *Oeotodus nakamurai* Nogami, 1967 from the Yencho Member of the Fengshan Fm. of northeast China. *Teridontus* was later reported from either the Upper Cambrian or Lower Ordovician (Landing et al., 1980; Miller, 1980; Landing and Barnes, 1981; Landing, 1983; An et al., 1983, 1985; Ni et al., 1983; Peng et al., 1983; Nowlan, 1985; Landing et al., 1986; Bagnoli et al., 1987; An, 1987; Buggisch and Repetski, 1987; Pohler and Orchard, 1990; An and Zheng, 1990; Seo and Ethington, 1993; Wang, 1993; Lehnert, 1994; Nicoll, 1994; Seo et al., 1994; Ji and Barnes, 1994; Taylor et al., 1996; Lehnert et al., 1997; Jia, 2000; Dubinina, 2000; Pyle and Barnes, 2002; Zeballo et al., 2005) sediments in numerous localities around the world, but a unanimous interpretation of the composition of the *Teridontus* apparatus organization was far from accepted.

In 2000 we were invited by J. J. Álvaro, E. P. Villas and D. Vizcaíno to join a working group on the stratigraphy of the Early Paleozoic of southern Montagne Noire (France). Our specific objective was the study of conodont faunas emerging from limestone intercalations in the Ordovician successions. Several samples from the Val d'Homs Formation collected in Sallèles-Caberdès, from Munio Formation, collected in Combes de Barroubio (St. Jean de Minervois) and, chiefly, from the St. Chinian Formation collected in La Regagnade Valley (St. Martial), produced an amazingly rich conodont fauna attributed to the *P. deltifer* Zone and, more precisely, to the lower part of the *P. deltifer deltifer* Subzone (Álvaro et al., 2005; Serpagli et al., 2007). The conodont assemblage has also yielded an extraordinarily abundant collection of well preserved elements belonging to a new species of *Teridontus* that is presented here. A more detailed analysis of the stratigraphic context, distribution and significance of the conodont fauna from southern Montagne Noire is the subject for another study and will be presented at a later date.

### THE GENUS *TERIDONTUS*

Two emended diagnoses of the genus *Teridontus* were provided independently in 1994. Ji and Barnes, describing Early Ordovician conodonts from Western Newfoundland, Canada (1994, p. 64) suggested that four element morphotypes (*a*, *b*, *c*, *e*) constituted the *Teridontus* multielement structure. According to the authors, the *a*, *b*, and *c* elements (equivalent respectively to Sc, Sb and Sa elements) were respectively symmetrical-subrounded, transitional and suberect-symmetrical whereas the *e* element (equivalent to M) was compressed. No elements in P positions were identified; furthermore, the early stages of the apparatus might have lacked *c*, *e* (Ji and Barnes, 1990, 1994), as well as *b* elements (Ji and Barnes, 1994).

Nicoll (1994, p. 371), based on a Late Cambrian conodont fauna from Queensland, Australia, regarded *Teridontus* as a seximembrate apparatus bearing two P (Pa and Pb) and four S (Sa, Sb, Sc and Sd) element types, but lacking an element in the M position.

Criteria used to discriminate *Teridontus* elements in the two

emendations are quite different. Ji and Barnes (1994) referred to the curvature of the cusp (suberect, reclined or recurved), cross section of the cusp and base, and presence of grooves or costae as main features to discriminate apparatus elements. According to Nicoll (1994), the length of the base (short in P and long in S elements) and the cross section of the basal margin were the major features used to segregate discrete element morphologies.

Zeballo et al. (2005), describing Tremadocian conodonts from Argentina, very recently provided a further emendation of *Teridontus*. The authors adopted the Ji and Barnes (1994) apparatus design, which better fitted with their material, but they included also a fifth morphotype (*f*) having a proclined cusp, straight anterior margin and triangular base profile. The difficulty in recognizing Nicoll's six morphotype apparatus structures was possibly attributed by the authors to the Late Cambrian age of Nicoll's and Nogami's original material, compared to the Early Ordovician age of their and of Ji and Barnes' material. On this basis, Zeballo et al. (2005) adopted a "sensu lato" designation for *T. nakamurai*, waiting for new data to come from further investigations.

Löfgren (1997a, 1997b, 1998, 1999a, 1999b) and Löfgren et al. (1999) in recent studies provided detailed reconstructions of several coniform apparatuses [e.g., *Semiacontiodus* (Miller, 1969); *Cornuodus* Fähræus, 1966; *Decoriconus peselephantis* (Lindström, 1955); *Variabiliconus* Landing, Barnes and Stevens, 1986] adopting the apparatus design that Nicoll had also accepted for *Teridontus*. In all such apparatuses, and in *Drepanodus* and *Cordylodus* as well, two P (Pa = g; Pb = f) elements are always present. This fundamental sexi- or septimembrate pattern seems in fact common in latest Cambrian and earliest Ordovician conodonts, either in coniform or ramiform apparatuses (e.g., *Cordylodus* Nicoll, 1990; *Jumudontus*, Nicoll, 1992; *Oepikodus*, Stewart and Nicoll, 2003, Nicoll and Ethington, 2003; *Erraticodon*, Nicoll and Kelman, 2004). On this basis, we see no reason why these elements should apparently be missing in *Teridontus*.

Our collection from the Montagne Noire, with the recovery of about 700 elements that can be assigned to a new species of *Teridontus*, strongly supports Nicoll's apparatus interpretation, as the six discrete morphologic types have also been recognized in our material. No elements with a laterally compressed cusp or bearing costae, carinae or grooves, diagnostic features of some of Ji and Barnes's morphotypes, have been identified in our specimens. Further considerations are discussed below and in the species diagnosis. The element designations used by Nicoll (1994), Löfgren (1997a, 1997b, 1998, 1999a, 1999b) and Löfgren et al. (1999) are regarded to be of the greatest use in recognizing and tracing similarities among the earliest conodont lineages (Löfgren, 1999a, p. 73), and this scheme is followed here.

As regards element curvature, in the Late Cambrian material *Teridontus nakamurai* has the "angle between the posterior margin of the cusp and the upper margin of base . . . essentially a right angle in all elements. The upper part of the cusp may be slightly recurved" (Nicoll, 1994, p. 372). A recent re-analysis of the original material by one of us (RSN) confirmed the absence of any curvature variability in all element types. On the contrary,

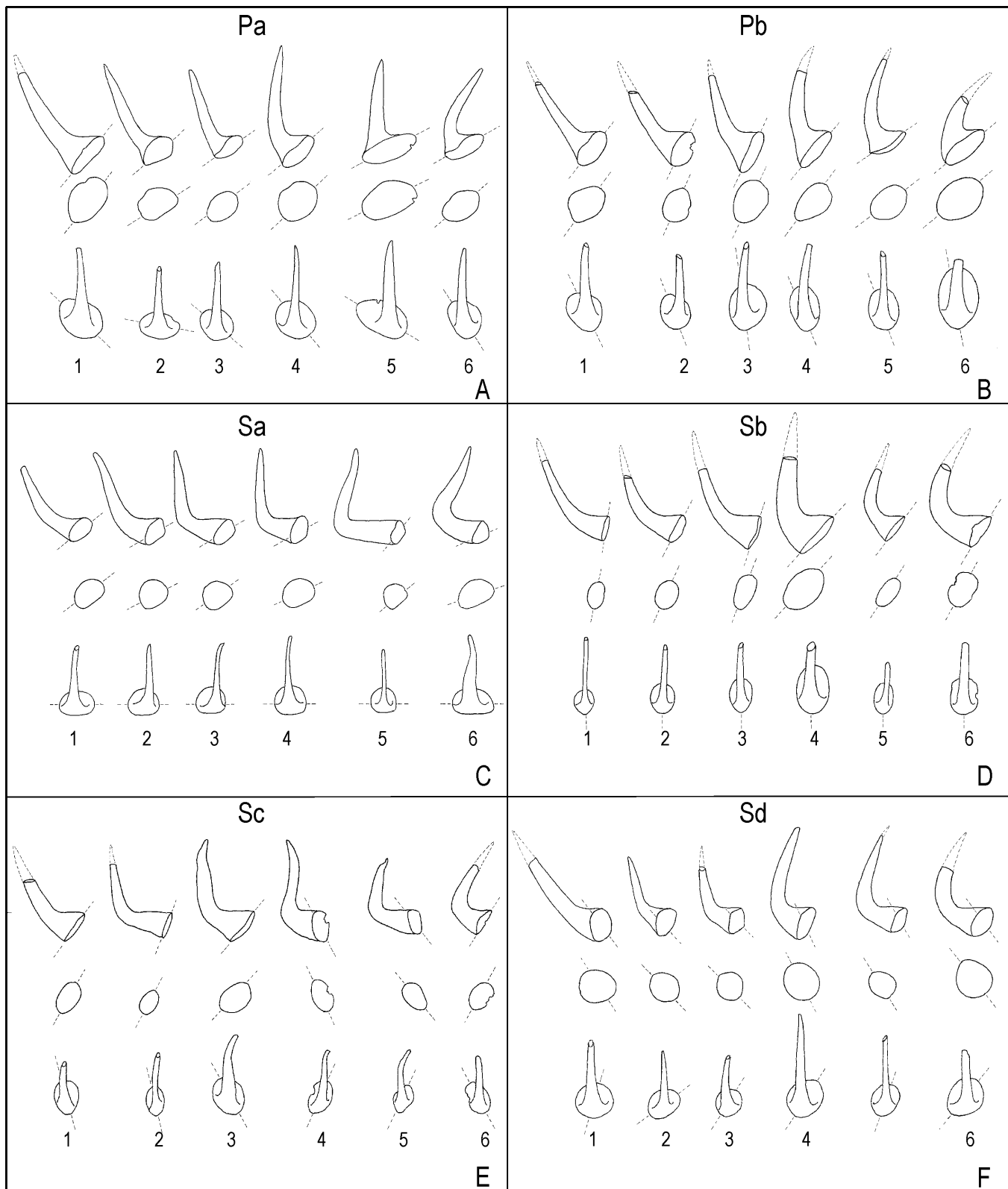


FIGURE 1—Element variability in *Teridontus gallicus* n. sp.

Early Ordovician *Teridontus nakamurai* elements may vary from “erect” (c) to “suberect to reclined” (a) or “reclined to recurved” (b and e elements) (Ji and Barnes, 1994, p. 65). Elements of *Teridontus gallicus* n. sp. reveal a strong curvature variability in each morphotype of the apparatus, with a gradual variation

from proclined to recurved elements via suberect, erect and reclined elements (Fig. 1). Proclined elements had been previously illustrated in *T. nakamurai* by several authors (Fig. 2). Most of them, interestingly, are Early Ordovician in age.

According to our criteria, the newly introduced *f* morphotype

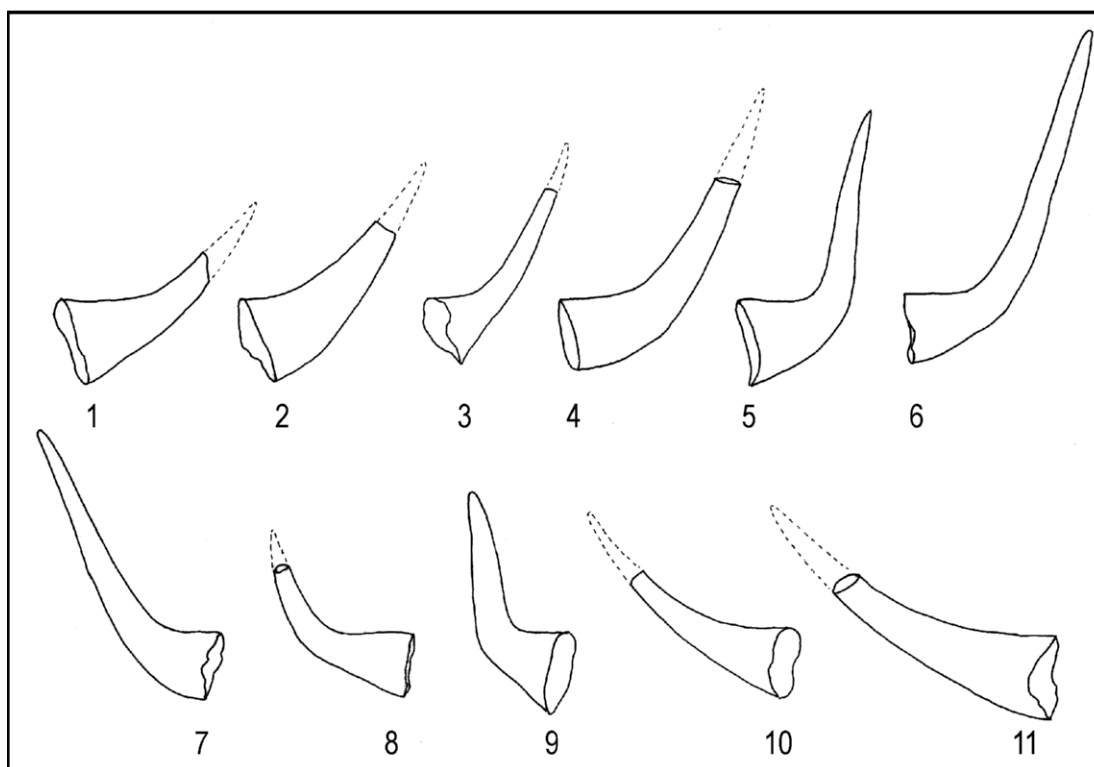


FIGURE 2.—Silhouettes of some proclined elements figured by former authors under *Teridontus nakamurai*. 1, Nowlan, 1985, fig. 5 (27) (earliest Ordovician-Canadian). 2, Wang Cheng-yuan (ed.), 1993, pl. 5, fig. 14 (Late Cambrian). 3, Buggisch and Repetski, 1987, pl. 8, fig. 14 (Tremadocian). 4, Landing and Barnes, 1981, pl. 1, fig. 15 (earliest Ordovician). 5, Bagnoli, Barnes and Stevens, 1987, pl. 2, fig. 18 (early Tremadocian). 6, Miller, 1980, pl. 2, fig. 15 (Late Cambrian). 7, Ji and Barnes, 1994, pl. 24, fig. 3 (earliest Ordovician-Canadian). 8, Dubinina, 2000, pl. 6, fig. 4 (Tremadocian). 9, Jia Cheng-Zao, 2000, pl. 9, fig. 22. 10, Pyle and Barnes, 2002, pl. 15, fig. 18 (earliest Tremadocian). 11, An Tai-Xiang and Zheng Zhao-Cheng, 1990, pl. 1, fig. 3.

of Zeballo et al. (2005) may better fit in Pa (or Pb) positions in the apparatus design here proposed.

#### SYSTEMATIC PALEONTOLOGY

The described and figured specimens are housed at the Paleontological Museum of the Dipartimento del Museo di Paleobiologia e dell'Orto Botanico of the University of Modena and Reggio Emilia (IPUM) under repository numbers IPUM 27884-27929.

#### Genus TERIDONTUS Miller, 1980

*Type species*.—*Oneotodus nakamurai* Nogami, 1967

*Emended diagnosis*.—Apparatus composed of six coniform elements differentiated into two P and four S elements. No M element has been recognized. The P elements have a relatively short base, but the bases of the S elements are relatively long. Discrimination of individual P and S types is based on the cross-section of the basal margin. The cusp is essentially round in cross-section, whereas the outline of the base is highly variable between element types. The angle between the upper margin of the base and the posterior margin of the cusp may be highly variable, especially in stratigraphically younger reports. All elements lack grooves, keels, or carinae. Fine striations have been noted on the surface of well-preserved specimens.

#### TERIDONTUS GALLICUS new species

Figures 1, 3–5

- Teridontus nakamurai* (Nogami). NOWLAN, 1985, p. 116, fig. 5.26–5.32.  
*Oneotodus? nakamurai* Nogami. LANDING, BARNES, AND STEVENS ?1986, pl. 1, figs. 1, 2.  
*Teridontus nakamurai* (Nogami). BUGGISCH AND REPETSKI, 1987, p. 159–160, pl. 2, figs. 1, 3–8, 10–17, 19–21; pl. 3, figs. 1–9, 16–20; pl. 8, figs. 13, 14; pl. 9, figs. 10, 14.

*Teridontus cf. nakamurai* (Nogami). BUGGISCH AND REPETSKI, 1987, pl. 2, figs. 2, 9, 18; pl. 3, figs. 10–15.

*Teridontus nakamurai* (Nogami). BAGNOLI, BARNES, AND STEVENS, 1987, pl. 2, figs. 17, 18; LEE, SEO, AND LEE, 1991, figs. 14, 15, 18.

*Parapanderodus* sp. KÜPPERS AND POHLER, 1992, fig. 5.2, 5.7.

*Oneotodus variabilis*. KÜPPERS AND POHLER, 1992, fig. 5.8–5.10.

*Teridontus nakamurai* (Nogami). WANG, (Ed.) ?1993, p. 211, pl. 5, figs. 13–18, 20–23; pl. 8, fig. 25; JI AND BARNES ?1994 (*a* elements only), pl. 24, figs. 1–3; DUBININA, 2000, p. 196, pl. 6, figs. 2, 4, 5, 7, 8.

*Teridontus nakamurai* s.l. (Nogami). ZEBALLO, ALBANESI, AND ORTEGA, 2005, p. 61, fig. 3A–E; ALBANESI AND ACENOLAZA, 2005, p. 304, 306, figs. 5 L–M.

*Diagnosis*.—A species of *Teridontus* characterized by a gradual variation from proclined to recurved elements *via* suberect, erect, reclined elements in each element type of the apparatus (Fig. 1). The basal cavity can be observed only in few well preserved elements and is restricted to the base with the pattern outlined by Nicoll (1994, text-fig. 3). All elements lack grooves, keels or carinae. Fine striations have been noted on the surface of well-preserved specimens (Figs. 3.13a, 4.2b).

Discrimination of individual P and S types is based on the cross-section of the basal margin of the element as follows:

**Pa element** (Fig. 1A)—Coniform asymmetrical element with short base obliquely compressed. Outline of basal cross-section irregularly oval with main axis strongly deflected to main axis of the cusp of an angle variable between 30 to 80 degrees.

**Pb element** (Fig. 1B)—Coniform asymmetrical element with short base laterally compressed. Outline of basal cross-section irregularly oval with main axis slightly deflected to main axis of the cusp of an angle variable between 10 to 30 degrees.

**Sa element** (Fig. 1C)—Coniform symmetrical element with

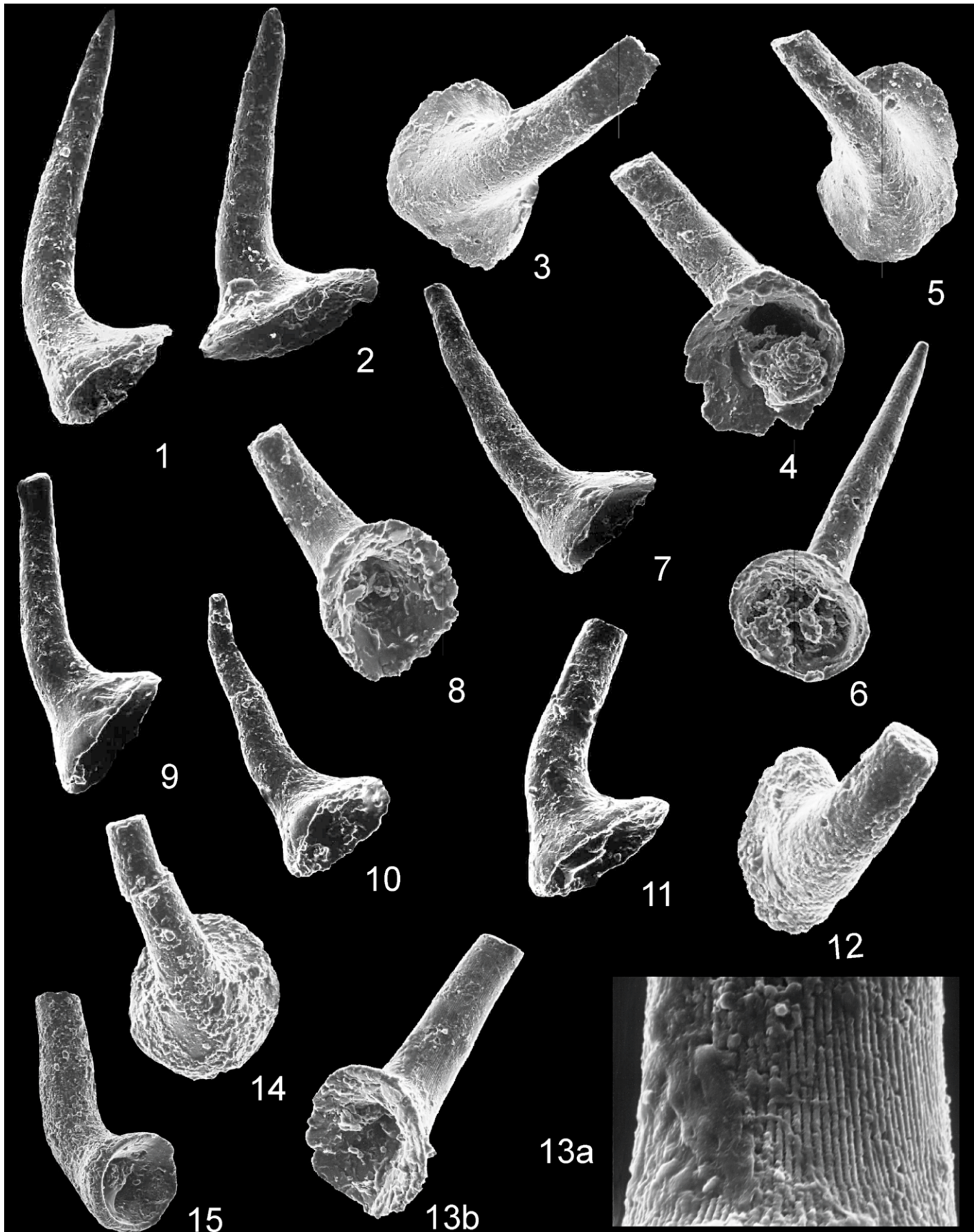


FIGURE 3—*Teridontus gallicus* n. sp. All elements from sample SM 1. 1–7, Pa elements; 1, IPUM 27884, lateral view,  $\times 180$ ; 2, IPUM 27885, lateral view,  $\times 140$ ; 3, IPUM 27886, anterior view,  $\times 130$ ; 4, IPUM 27887, lower-posterior view,  $\times 150$ ; 5, IPUM 27888, anterior view,  $\times 120$ ; 6, IPUM 27889, posterior view,  $\times 150$ ; 7, IPUM 27890, lateral view,  $\times 110$ . 8–15, Pb elements. 8, IPUM 27891, posterior view,  $\times 170$ ; 9, IPUM 27892, lateral view,  $\times 140$ ; 10, IPUM 27893, postero-lateral view,  $\times 120$ ; 11, IPUM 27894, lateral view,  $\times 140$ ; 12, IPUM 27895, antero-lateral view,  $\times 200$ ; 13, IPUM 27896, a, fine striations,  $\times 750$ , b, postero-lateral view,  $\times 130$ ; 14, IPUM 28797, anterior view,  $\times 130$ ; 15, IPUM 28798, postero-lateral view,  $\times 120$ .

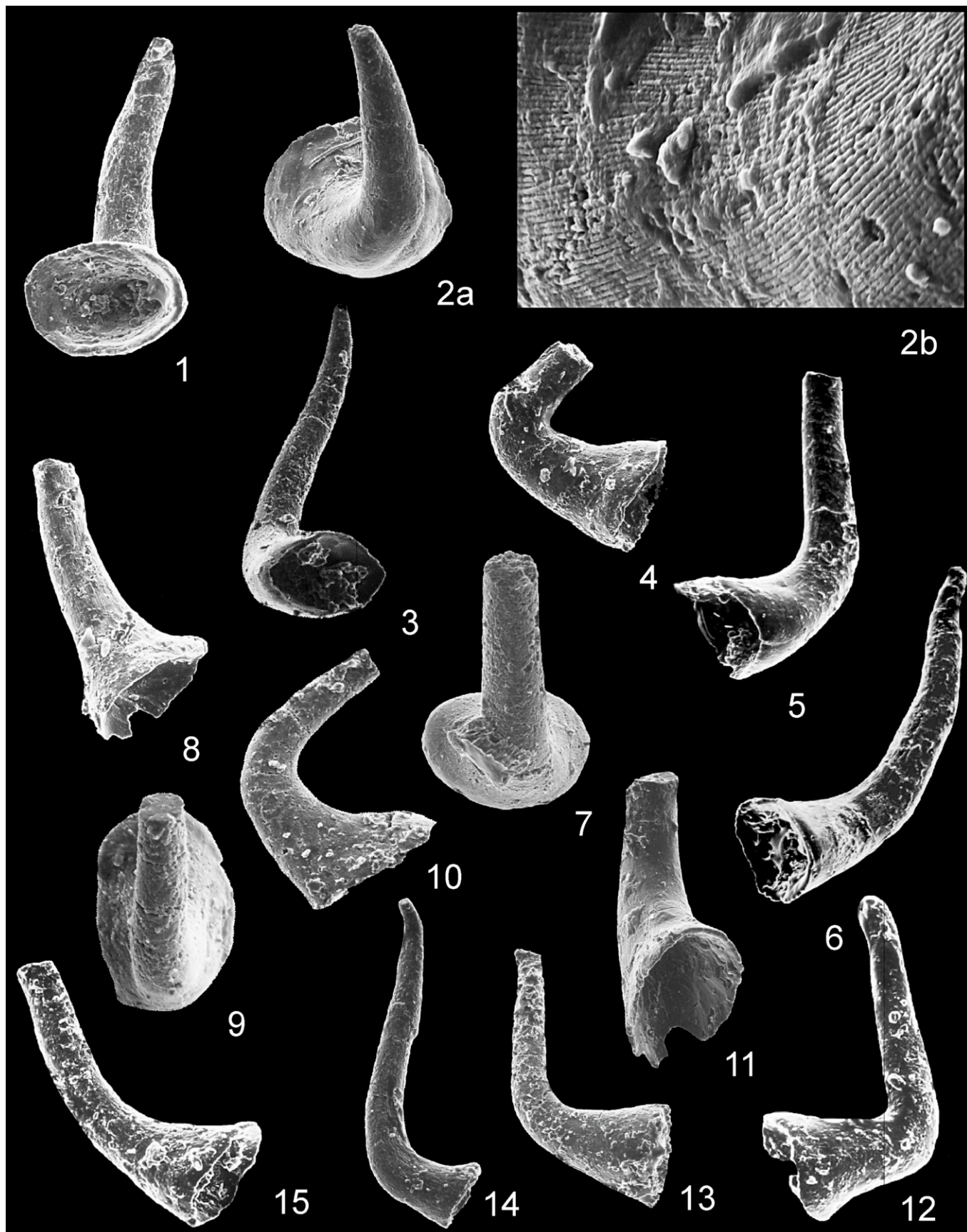


FIGURE 4—*Teridontus gallicus* n. sp. All elements from sample SM 1. 1–8, Sa elements. 1, IPUM 27899, posterior view,  $\times 150$ ; 2, IPUM 27900, a, antero-lateral view,  $\times 120$ , b, detail of fine striations,  $\times 850$ ; 3, IPUM 27901, postero-lateral view,  $\times 160$ ; 4, IPUM 27902, lateral view,  $\times 130$ ; 5, IPUM 27903, lateral view,  $\times 150$ ; 6, IPUM 27904, lateral view,  $\times 150$ ; 7, IPUM 27905, anterior view,  $\times 170$ ; 8, IPUM 27906, lateral view,  $\times 135$ . 9–15, Sb elements. 9, IPUM 27907, anterior view,  $\times 220$ ; 10, IPUM 27908, lateral view,  $\times 170$ ; 11, IPUM 27909, posterior view,  $\times 120$ ; 12, IPUM 27919, lateral view,  $\times 150$ ; 13, IPUM 27911, lateral view,  $\times 140$ ; 14, IPUM 27912, lateral view,  $\times 170$ ; 15, IPUM 27913, postero-lateral view,  $\times 150$ .

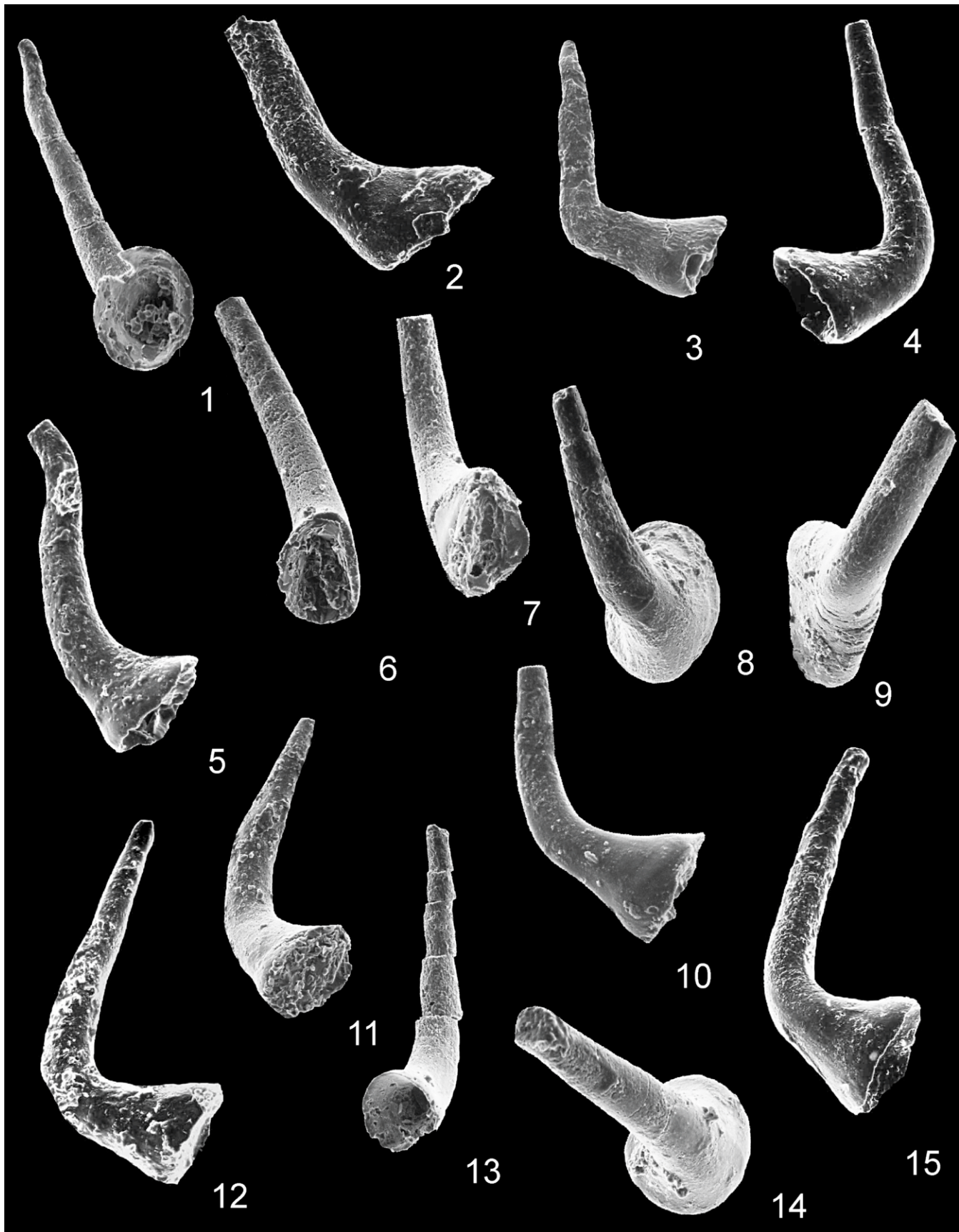


FIGURE 5—*Teridontus gallicus* n. sp. All elements from sample SM 1. 1–8, Sc elements. 1, IPUM 27914, posterior view,  $\times 165$ ; 2, IPUM 27915, lateral view,  $\times 125$ ; 3, IPUM 27916, lateral view,  $\times 105$ ; 4, IPUM 27917, lateral view,  $\times 170$ ; 5, IPUM 27918, lateral view,  $\times 135$ ; 6, IPUM 27919, posterior view,  $\times 150$ ; 7, IPUM 27920, posterior view,  $\times 170$ ; 8, IPUM 27921, antero-lateral view,  $\times 130$ . 9–15, Sd elements. 9, IPUM 27922, anterior view,  $\times 160$ ; 10, IPUM 27923, lateral view,  $\times 165$ ; 11, IPUM 27924, postero-lateral view,  $\times 155$ ; 12, IPUM 27925, lateral view,  $\times 145$ ; 13, IPUM 27926, postero-lateral view,  $\times 120$ ; 14, IPUM 27927, anterior view,  $\times 150$ ; 15, IPUM 27928, lateral view,  $\times 130$ .

long base dorso-ventrally compressed. Subrounded basal cross-section with main axis perpendicular to main axis of the cusp.

**Sb element** (Fig. 1D)—Coniform sub-symmetrical element with long base laterally compressed. Ovate basal cross-section with main axis more or less coincident with main axis of the cusp.

**Sc element** (Fig. 1E)—Coniform asymmetrical element with long base irregularly laterally compressed. Irregular ovate basal cross-section having main axis slightly deflected to main axis of the cusp of an angle variable between 10 to 35 degrees.

**Sd element** (Fig. 1F)—Coniform asymmetrical element with long base slightly obliquely compressed. Irregularly rounded basal cross-section with main axis more or less deflected to main axis of the cusp of an angle variable between 15 to 60 degrees.

*Etymology.*—From Gallia, the Latin name for France, area of topotypic material.

*Type.*—Holotype, IPUM 27890, Figure 3.7. Sample SM 1, Tremadocian (lower part of the *P. deltifer deltifer* Subzone).

*Type locality and horizon.*—La Regagnade Valley (in the vicinity of St. Martial; lenticular limestone, up to 10 cm thick, located at the lowermost part of the Saint-Chinian Formation, ca. 25 m above the top sandstones of the underlying La Dentelle Formation (Álvaro et al., 2003); Early Ordovician (Tremadocian, *Paltodus deltifer deltifer* Subzone of the *P. deltifer* Zone and *Shu-mardia* (*C.*) *pusilla* Zone).

*Other material examined.*—679 elements.

*Discussion.*—The large morphologic variation in the Montagne Noire *Teridontus* population is the basis for this proposal of a new species. Such variability has already been noted by Buggisch and Repetski (1987) under *T. nakamurai* with the illustration of 35 specimens.

As already pointed out, the composition of the apparatus of *T. gallicus* n. sp. suggested by the Montagne Noire material (six elements types and no M element) is consistent with Nicoll's reconstruction as well as with several Late Cambrian and Early Ordovician coniform apparatuses. However, unlike *T. nakamurai* in which there is very little morphologic variation of the cusp within each element type, in *T. gallicus* n. sp. there is a great deal of variation in cusp inclination. The recognition of the element types is not always simple, in part owing to elements with imperfect preservation, especially broken basal margins, but also to the existence of intermediate forms in all P and S element morphotypes. Nevertheless, the great number of morphologies that we include in *T. gallicus* n. sp. suggests also a need for reconsideration the validity of most of the elements included in the genus *Teridontus*. In a few specimens, particularly inside the Sa and Sc sequences, the distal part of the cusp may assume some terminal twisting, possibly due to metamorphic deformation. The emended diagnoses presented by Ji and Barnes (1994) and Zeballo et al. (2005) have been already discussed in detail above.

The main differences between *T. gallicus* n. sp. and *T. nakamurai* are as follows:

1. Nicoll (1994) has shown that in the large population of Late Cambrian *T. nakamurai* of Australia all elements have an essentially right angle between the posterior margin of the cusp and the upper margin of the base, with only the upper part of the cusp that may be slightly recurved. That means that proclined elements were never found among the 1066 specimen studied. Therefore, the "true" *nakamurai* lacks the variability which characterises our new species.
2. Possibly much of the Ordovician *Teridontus* material should be assigned to the new species proposed here, characterised by variability of curvature whereas the latest Cambrian, and

possibly the earliest Ordovician, material remains in *T. nakamurai*.

3. In *T. nakamurai* the distribution of white matter (albid tissue) in the cusp, except the hyaline tip, is very uniform and with an abrupt transverse and planar transition to a hyaline base, as it is well illustrated by the sketches supplied by Nicoll (1994, fig. 3). The preservation of our material makes it difficult to establish the separation between albid and hyaline tissue.

Comments on the synonymy list are given below.

Nowlan (1985, p. 116) described and illustrated several "markedly reclined" and "strongly proclined" specimens in his fauna. Except for two specimens, all of them were recovered from the Ordovician part of the sections (upper part of Cass Fiord and Cape Clay formations). Possibly also some specimens identified as *T. aff. T. nakamurai* belong to *T. gallicus*.

Buggisch and Repetski (1987, p. 159) stressed the great morphological variation in their Early Ordovician material from Antarctica, documented with the illustration of 35 specimens. In our opinion, 14 specimens identified by the authors as *T. cf. nakamurai* should be assigned to *T. gallicus* n. sp., thus including the full range of morphologic variability diagnostic of the new species.

Bagnoli et al. (1987) figured two specimens from Tremadocian beds of Western Newfoundland one of which (pl. 2, fig. 18) seems to fit well in the Sb sequence of *T. gallicus* n. sp.

Neither of the two figured specimens reported by Landing, Barnes and Stevens (1986, pl. 1, figs. 1, 2) from the Tremadocian of Quebec is suberect as in typical *T. nakamurai*, but one is proclined and one reclined.

All three specimens from the Early Ordovician of Korea and figured by Lee et al. (1991) fit in the variability of our new species.

Some Montagne Noire specimens figured by Küppers and Pohler (1992) as *Parapanderodus* sp. (fig. 5.2, 5.7) or as *Oneotodus variabilis* (fig. 5.8–5.10) may match our concept of *T. gallicus* n. sp.

In spite of the high variability illustrated by the Chinese specimens reported by Wang (ed., 1993), they are considered with doubts in the synonymy list owing to their Late Cambrian age.

Only a few specimens of Ji and Barnes (1994, pl. 24) may belong to *T. gallicus* n. sp. Much of the material studied by Ji and Barnes probably does not belong within *Teridontus*. The specimens with laterally compressed cusps (Ji and Barnes, 1994, pl. 24, figs. 6–9, 16–17 and 22–25) certainly do not belong in the genus, nor does the element with a lateral groove (pl. 24, fig. 4).

Dubinina (2000) reported several specimens from the Early Ordovician of Central Asia which show high variability and might belong to our new species.

Zeballo et al. (2005) figured two proclined elements (*f* element of fig. 3E: moderately proclined and *c* element of fig. 3C: strongly proclined) in their fauna.

Albanesi and Acenolaza (2005) did not illustrate any proclined specimen in their fauna to document the diagnostic curvature variability of our new species. Their material comes from the same formation yielding "*T. nakamurai*" specimens sensu Zeballo et al. (2005) and it is highly probable it may belong to *T. gallicus* n. sp.

*Occurrence.*—*T. gallicus* n. sp. has a wide distribution, having being recovered from numerous Early Ordovician localities around the world, including Antarctica (Wright et al., 1984; Buggisch and Repetski, 1987), but, as far as we know, it has been reported in Europe only as *Parapanderodus* sp. and *Oneotodus variabilis* by Küppers and Pohler (1992).

The stratigraphic occurrence of the Montagne Noire elements in the *P. deltifer deltifer* Subzone represents the youngest report of *Teridontus*. This genus, in fact, reaches the *P. deltifer pristinus* Subzone in Argentina (Albanesi et al., 2005; Zeballo et al., 2005) and the claimed occurrence in the lowest Boat Harbour Fm. in Newfoundland, equivalent to *P. deltifer* Zone (Ji and Barnes, 1994, p. 65) needs clarification, as it is not confirmed by distribution reported in tables of pages 91, 92 as well as in text-fig. 21.

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