



Morphologic variation in the P1 element of Mississippian species of the conodont genus *Pseudognathodus*

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ABSTRACT

A revision of the Austin Conodont Collection at the Natural History Museum, London, has revealed a diverse assemblage of P1 elements of *Pseudognathodus*. *Pseudognathodus homopunctatus*, *Ps. lineatus*, *Ps. mermaidus* and *Ps. symmutatus* are differentiated and a new species, *Ps. posadachaconae*, is defined from material from North Wales. The systematic of these species is updated. A revised diagnosis is provided for the genus *Pseudognathodus*, as well as for the species *Ps. lineatus* and *Ps. symmutatus*. The types of *Ps. symmutatus* cannot be differentiated from immature specimens of *Ps. homopunctatus*. The evolutionary relationships of *Pseudognathodus* species are discussed. Stratigraphic distribution indicates that diversity increased moderately from the upper Tournaisian and lower Viséan to the upper Viséan (Mississippian, Carboniferous). *Pseudognathodus homopunctatus* and *Ps. symmutatus* are widely distributed palaeogeographically whereas *Ps. lineatus* and *Ps. posadachaconae* sp. nov. are endemic.

Keywords: Conodont, *Pseudognathodus*, systematics, Mississippian, Viséan.

RESUMEN

Una revisión de los conodontos de la Colección Austin del Museo de Historia Natural en Londres ha puesto de manifiesto la diversidad de los elementos P1 de *Pseudognathodus*. Además de las especies *Ps. homopunctatus*, *Ps. lineatus*, *Ps. mermaidus* y *Ps. symmutatus*, una especie nueva, *Ps. posadachaconae*, es propuesta para ejemplares del Norte de Gales. La sistemática de todas las especies del género es revisada e incluye una diagnosis para el género *Pseudognathodus* y para las especies *Ps. lineatus* and *Ps. symmutatus*. Los tipos de *Ps. symmutatus* no pueden ser distinguidos de los ejemplares inmaduros de *Ps. homopunctatus*. Se discuten las relaciones evolutivas entre las distintas especies de *Pseudognathodus*. La distribución estratigráfica de las mismas indica un incremento moderado en la diversidad del género desde el Tournaisiense superior y el Viseense inferior al Viseense superior (Misisípico, Carbonífero). *Pseudognathodus homopunctatus* y *Ps. symmutatus* tuvieron una distribución paleogeográfica extensa, mientras que *Ps. lineatus* y *Ps. posadachaconae* sp. nov. fueron especies endémicas.

Palabras clave: Conodonto, *Pseudognathodus*, sistemática, Misisípico, Viseense.

1. INTRODUCTION

Gnathodus commutatus homopunctatus Ziegler has been used to identify the base of the Viséan, Mississippian (Devuyst *et al.*, 2003). P1 elements of this taxon are morphologically similar to *Gnathodus symmutatus* Rhodes *et al.*, and *G. symmutatus mermaidus* Austin & Husri, although their identification has been subject to much discussion. Metcalfe (1980) included the three taxa in *G. homopunctatus* based on their similarity and coeval presence along similar stratigraphic ranges. Austin & Husri (1975) considered them to be three subspecies of *G. symmutatus*, whereas many authors recognise three valid species assigned by Stone (1991) to the so-called *homopunctatus* group. The original designation of this group to the genus *Gnathodus* Pander was also questioned with Stone (1991) naming it informally *Gnathodus sensu lato*. Park (1983) had previously included these species in the genus *Pseudognathodus nomen nudum*. Dzik (1997) included them in *Protognathodus* Ziegler, based on the similarity of the P1 element, whereas Barskov *et al.* (1987), and Tian & Coen (2005), among others, preferred to assign them to *Paragnathodus* Higgins, a junior synonym of *Lochriea* Scott. Atakul-Özdemir *et al.* (2012) following cladistic analysis, considered *G. homopunctatus* to belong to *Lochriea* based on the co-occurrence of discrete elements of the apparatus of *Lochriea* with mature P1 elements of *G. homopunctatus* in three samples from Lancashire (United Kingdom).

In our opinion, the *G. homopunctatus* group (*sensu* Stone, 1991) additionally comprises specimens from the Viséan of Ireland differentiated by Austin & Husri (1975) as *G. commutatus lineatus* sp. nov. and *G. commutatus multinodosus* Higgins, *nomen nudum*, which currently belongs to *Lochriea multinodosa* (Wirth). Ronald Austin's Collection housed in the Natural History Museum, London (NHMUK), includes the type specimens of *G. symmutatus*, *G. symmutatus mermaidus*, and *G. commutatus lineatus*, as well as many specimens in assemblage slides showing the morphologic variation of the P1 element in the *G. homopunctatus* group. The aims of this work are to review this morphologic variation and to update the systematic of this species group. We conclude that they belong to the genus *Pseudognathodus* Perret. We have focused on the morphology of the P1 element, as there seems to be sufficient variation to differentiate the genus, although the validity of the species in this genus should be supported by more data about the other elements forming the apparatus.

2. MATERIALS AND METHODS

This study concentrated on the type and figured material in Ronald Austin's Collection housed in the NHMUK but also included specimens picked from assemblage slides

deposited later in 1993. Rhodes *et al.* (1969) studied *Pseudognathodus symmutatus* from samples CYD 7 to 3D 14/15 at Craig-y-Dinas and Melte Bridge in the North Crop of the Coalfield of the South Wales. The taxon was associated with *Pseudognathodus homopunctatus*, *Lochriea mononodosa* (Rhodes *et al.*), and *Gnathodus girty collinsoni* Rhodes *et al.* in upper Brigantian beds (upper Viséan to lower Serpukhovian, Mississippian) according to Higgins (1985, table 6). In these samples, specimens of *Ps. symmutatus* (42 elements) are smaller than those of *Ps. homopunctatus* (146 elements).

Elements assigned to *Ps. homopunctatus* and *Ps. symmutatus* were studied by Aldridge *et al.* (1968) in Flintshire (North Wales; 56 elements). Samples were collected from the Moel Hiraddug Limestone to the Prestatyn Limestone (Regional upper Arundian to upper Asbian substages, Viséan) according to Somerville *et al.* (1986). The abundance of conodonts in these samples is relatively low.

Austin & Husri (1975) described a wide variation from sections in counties Limerick and Clare (Republic of Ireland), where they differentiated *Ps. homopunctatus* (544 elements), *Ps. symmutatus* (406 elements), and, of particular interest to this study, *Ps. mermaidus* (84 elements), *G. c. lineatus* (56 specimens), and *G. c. multinodosus* (15 elements). Samples from County Limerick were collected from the Rathkeale and Corgrig Lodge formations that are upper Chadian to Brigantian (Viséan). Samples from County Clare (west of the River Fergus and islands in the estuary of the Shannon) correspond to similar stratigraphic interval as the Limerick area, between the Mermaid and the Inishtubrid Beds (Austin & Husri, 1975).

It is difficult to investigate the species concepts of Austin & Husri (1975) from their assemblage slides as many of the specimens, apart from the figured specimens, are loose. Slide labels include abbreviated notations in pencil (eg. "G. homo", "G. merma", "G. line", "G. multi") that seem to correspond to the previous determinations by Austin & Husri (1975). Another difficulty is the occurrence of secondary apatite and calcite overgrowths on many of the specimens (irregular envelope microtexture after Blanco-Ferrera *et al.*, 2011). This envelope may mask or modify the observation of ornamentation of the cup. The overgrowth and original relief of the cup can only be seen by magnification and observation under a scanning electronic microscope (SEM). Specimens were selected for observation and illustration in the Core Research Laboratories (Imaging and Analysis Centre) of the NHMUK using a Hitachi S-2500 scanning electron microscope. Unfortunately, one of the aluminum stubs was damaged during the Au-coating process, prior to SEM study. All of the specimens on the stub were lost including the paratype (NHMUK PM X 1754) and the holotype (NHMUK PM X 1755) of *G. symmutatus mermaidus* (Austin & Husri, 1975, pl. 2, fig. 11 and pl. 4, fig. 10, respectively) and the holotype

(NHMUK PM X 1723) and paratype (NHMUK PM X 1724) of *G. commutatus lineatus* (Austin & Husri, 1975, pl. 2, fig. 9 and pl. 4, fig. 11). Other characteristic specimens were chosen and have been illustrated as part of this study.

Pseudognathodus homopunctatus is very abundant in a bed of nodular cephalopod-bearing limestone of the Mississippian Alba Formation at the Portillas del río Nevandi (Cantabrian Mountains, Spain). A few elements have been used to illustrate ornamentation changes during ontogeny. Illustrated conodonts from this sample are housed in the Department of Geology Museum of the University of Oviedo (abbreviated prefix DGO in the catalogue number). The rest of the illustrated material is housed at the Natural History Museum in London (NHMUK). The notation and orientation applied in the conodont descriptions follow Purnell *et al.* (2000).

3. SYSTEMATICS

Order **OZARKODINIDA** Dzik, 1976

Family **Gnathodontidae** Sweet, 1988

Genus *Pseudognathodus* Perret, 1993

Type species *Gnathodus homopunctatus* Ziegler, 1960, by original designation.

Diagnosis. Modified from Park (1983). P1 element with a distal outline of the cup from ellipsoidal to sub-triangular; the widest part at the ventral cup. Ornamentation may be lacking on a low cup that may show a swollen area close to the carina in the proximal cup, or a terrace with a stepped margin surrounded by a veil (term for the marginal flared area after Purnell & von Bitter, 1992). Ornamentation varies from a few nodes, to a row of nodes or transverse ridges on each side of the cup, or to a group of nodes. The dorsal (adaxial) outline shows a curved outline. The highest denticles are in the central part of the ventral blade, but not at the ventral margin. In some species, the highest denticles are in the dorsal part of the blade.

Remarks. Park (1983) included *Gnathodus commutatus homopunctatus* Ziegler and *Gnathodus symmutatus* Rhodes *et al.*, in a new genus, *Pseudognathodus*, characterised by the lack of a caudal parapet and a semi-elliptical oral outline. The proposal did not satisfy the requirements of publication specified by the International Commission on Zoological Nomenclature (1999, Article 9.12). Nevertheless, Perret (1993) described and adopted the genus *Pseudognathodus* Park including *Ps. homopunctatus* and *Ps. symmutatus* and was followed by other authors (Perret *et al.*, 1994; Skompski, 1996; Perri & Spalleta, 1998; Meischner & Nemyrovska, 1999; Kullmann *et al.*, 2008; see synonymy

list of *Ps. homopunctatus*). Only Park (1983) included diagnosis for the genus. On basis of the differences of P1 elements with respect to other genera, we have cautiously assumed the validity of the genus *Pseudognathodus* for the present study, but suggest that more data is needed about the other elements forming the apparatus to confirm this.

Protognathodus Ziegler is homeomorphic with *Pseudognathodus*. Both show a subsymmetrical or symmetrical cup with an ellipsoidal outline of the cup and ornamentation lacking, few nodes or rows of nodes in each half of the cup (Fig. 1d). The descendant species of *Protognathodus*, *Gnathodus* Pander has a distinct asymmetrical cup with the narrow caudal half variably ornamented. The oral or adaxial outline of the blade-carina in *Protognathodus* and *Gnathodus* shows a high blade to the ventral end with the highest denticles. The outline of denticles on the blade-carina forms a continuous curve that dorsally decreases in height, (Figs 1e, 1h–1i). At the ventral end of the blade, lower denticles and a shorter blade is observed, particularly in small specimens, and in several species (Fig. 1h). The dorsal outline of *Pseudognathodus* decreases in height towards the dorsal and ventral ends according to Park (1983) and Perret (1993) (Figs 1a–1c). There may be one or several lower denticles on the ventral blade (Figs 1a–1c) but the decreasing height of the ventral blade is a useful character to differentiate *Pseudognathodus*. However, this characteristic may be less marked in large specimens of *Pseudognathodus* where high denticles are very close at the ventral end of the free blade (see Figure 2f in Atakul-Özdemir *et al.*, 2012). Furthermore, the denticles may be fused as a ridge in the proximal area (just above the basal cavity) in specimens of both genera (Figs 1b–1c, 1h–1i). Stone (1991) used *Gnathodus sensu lato* because of the similarity to gnathodontids.

Species of *Lochriea* Scott show a high ventral blade, with the highest denticles normally close to the ventral margin (Figs 1j–1m). The dorsal outline may decrease in height in immature specimens or oldest species of the genus (*Lochriea saharae* Nemyrovska *et al.*), but the dorsal termination is high with a straight margin in other species and in mature elements. Furthermore, P1 elements of *Lochriea* have a lower number of denticles, which that are triangular in outline and only isolated at the tips (Fig. 1j). The cup is wide on either side of the blade, increasing in width with the development of ornamentation concentrated in the transverse, swollen, proximal areas with a transverse disposition. The expansion of the cup is mostly along the rostral-caudal axis and characteristically asymmetric in ornamented species. The rostral side is more expanded than the caudal. The caudal margin is only slightly expanded close to the dorsal margin and forms a curved sinus from the second or third denticle of the carina. Atakul-Özdemir *et al.* (2012) considered *G. homopunctatus* to be within *Lochriea*, based on a cladistic analysis of co-occurring discrete elements of the apparatus and mature

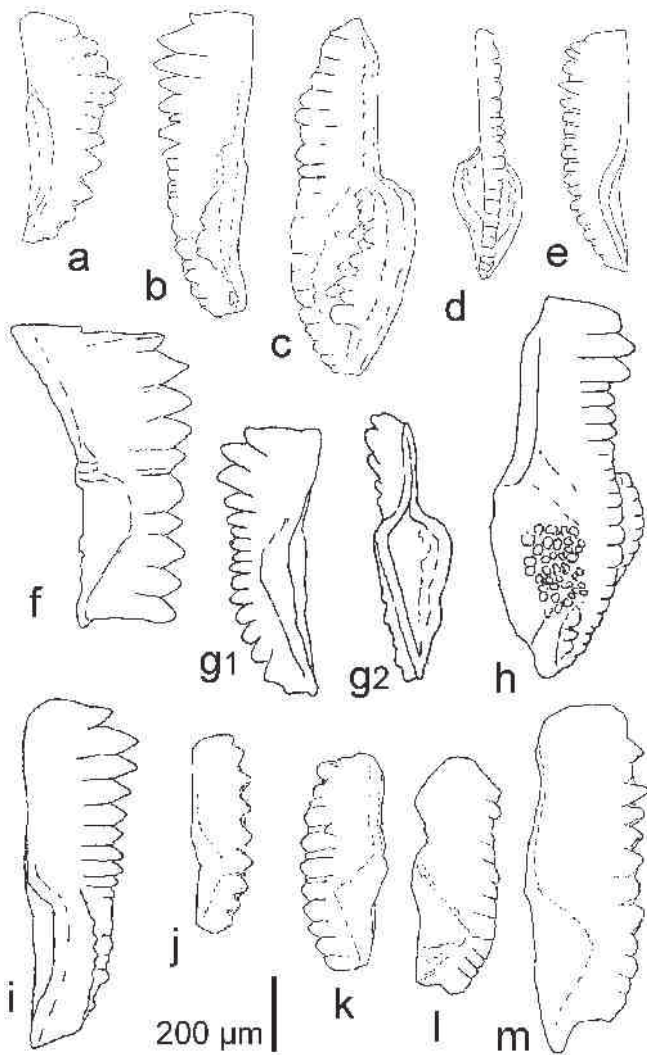


Figure 1. Outline drawings from various publications of P1 elements in lateral views. **a)** *Pseudognathodus symmutatus* (Rhodes *et al.*), NHM PM X 1750, sample L. 7 after Austin & Husri (1975, pl. 4, fig. 7a). **b)** *Pseudognathodus homopunctatus* (Ziegler), NHMUK PM X1752, sample L. 7 after Austin & Husri (1975, pl. 4, fig. 9c). **c)** *Pseudognathodus lineatus* (Austin & Husri), NHMUK PM X 1725, sample Cl. 12B from Austin & Husri (1975, pl. 2, fig. 13). **d)** *Protognathodus cf. collinsoni* Ziegler, SLU 406 after Chauffe & Nichols (1995, pl. 2, fig. 32). **e)** *Protognathodus meischneri* Ziegler, SLU 403 after Chauffe & Nichols (1995, pl. 2, fig. 33). **f–g2)** *Cudotaxis pricesilingi* Chauff, holotype SUI 45239 and paratype SUI 45238 after Chauff (1981, pl. 3, figs 25, 26 and 30). **h)** *Gnathodus bilineatus* (Roundy), NHMUK PM X 1717, sample D after Austin & Husri (1975, pl. 3, fig. 7c). 16. **i)** *Gnathodus girtyi* Hass, NHMUK PM X 1738, sample B. 14 after Austin & Husri (1975, pl. 3, fig. 3b). **j–l)** *Lochriea commutata* (Branson & Mehl), NHMUK PM X 1719– NHMUK PM X 1721, sample L. 10 the first and L. 7 for the others after Austin & Husri (1975, pl. 2, figs 1c, 2c and 3c). **m)** *Lochriea scotiaensis* (Globensky), NHMUK PM X1722, sample Cl. 12B after Austin & Husri (1975, pl. 2, fig. 12c).

P1 elements in three samples from Lancashire. Elements of the apparatus of *Lochriea* occur without P1 elements of *Lochriea* but with P1 of *G. homopunctatus* (Atakul-Özdemir *et al.*, 2012). However, this hypothesis is based on a small number of elements per sample (11 P1 of *Ps. homopunctatus* / 2 P2, 3 M and 5 S of *Lochriea* in sample BSG 20680; 6 P1 / 1 M in BSG 20684; 12 P1 / 2 M in BSG 26086 according to their table 1). Atakul-Özdemir *et al.* (2012) studied samples from the English Arundian (early Viséan), and other British Arundian sections yielded P1 elements of *Lochriea commutata* and *L. saharae* (Stone, 1991). Consequently, the apparatus structure of *Ps. homopunctatus* needs be confirmed.

Cudotaxis Chauff is a Tournaisian genus from North America (Chauff, 1981, pl. 3, figs 25–26, 30–32) that shows an expanded and wide dorsal cup (Figs 1f–1g2), although it could be a morphologic convergence with *Pseudognathodus*. Immature elements of *Cudotaxis pricesilingi* Chauff show a convex outline of the denticle tips similar to *Pseudognathodus* (Fig. 1g1). However, the denticulation is more irregular than in *Pseudognathodus*, with lower and smaller denticles in the middle of the element. Strong and deeply inserted denticles are present in strongly arched mature elements (Fig. 1f).

Pseudognathodus homopunctatus (Ziegler, 1960)
(Figs 1b, 2a1–2m, 4b)

1957 *Gnathodus commutatus punctatus*, Bischoff, p. 24, pl. 4, figs 7–11, 14.

*1960 *Gnathodus commutatus homopunctatus*, Ziegler, p. 5, pl. 4, fig. 3.

1961 *Gnathodus commutatus* Branson & Mehl var. *homopunctatus* Bischoff, Higgins, pl. 10, fig. 9.

1962 *Gnathodus commutatus homopunctatus*, Ziegler, p. 395, pl. 4, fig. 3.

1962 *Gnathodus commutatus homopunctatus*, Higgins, pl. 2, fig. 21.

? 1965 *Gnathodus commutatus homopunctatus*, Spassov, p. 159, pl. 3, fig. 13.

1967 *Gnathodus commutatus homopunctatus*, Wirth, p. 206, 207, pl. 19, fig. 12.

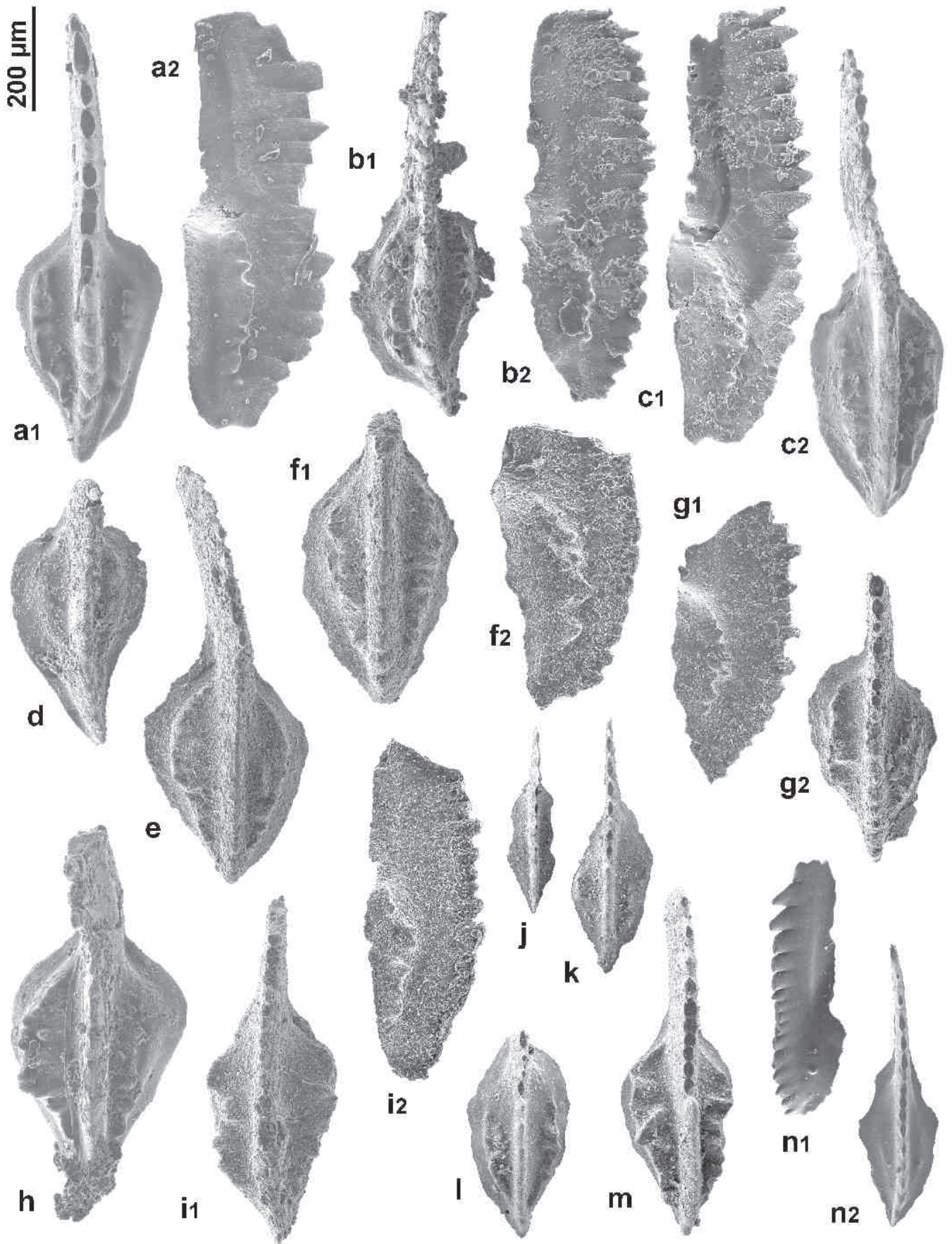
P 1967 *Gnathodus commutatus homopunctatus*, Spassov & Filipović, p. 62, pl. 8, fig. 3 (only).

1969 *Gnathodus commutatus homopunctatus*, Spassov *et al.*, p. 159, pl. 3, fig. 17.

1969 *Gnathodus commutatus* (Branson & Mehl), Thompson & Goebel, p. 23–24, pl. 4, figs 4, 6, 7.

v 1969 *Gnathodus homopunctatus*, Rhodes *et al.*, p. 103, pl. 19, figs 5a–8d.

- 1970 *Gnathodus commutatus homopunctatus*, Reynolds, p. 10, pl. 1, fig. 8.
- 1973 *Gnathodus homopunctatus*, Igo, p. 194, pl. 29, figs 18–21.
- v 1973 *Gnathodus homopunctatus*, Austin & Aldridge, pl. 1, fig. 2.
- 1974 *Gnathodus* sp., Mathews & Thomas, pl. 51, figs 4, 8–9.
- 1974 *Gnathodus commutatus homopunctatus*, Mathews & Thomas, pl. 51, fig. 6.
- v 1975 *Gnathodus symmutatus homopunctatus*, Austin & Husri, pl. 4, figs 1, 9, 12.
- p v 1975 *Gnathodus symmutatus symmutatus* Rhodes *et al.*, Austin & Husri, pl. 4, figs 6a–6b (only).
- 1975 *Gnathodus homopunctatus*, Higgins, p. 33–34, pl. 7, figs 1–6; pl. 10, fig. 7.
- 1976 *Gnathodus symmutatus homopunctatus*, Bless *et al.*, pl. 14, figs 6, 8–10.
- 1976 *Gnathodus* cf. *homopunctatus*, Groessens in Conil *et al.*, pl. 6, figs 14–15.
- 1977 *Gnathodus* cf. *homopunctatus*, Groessens & Noël, pl. 1.
- 1977 *Gnathodus homopunctatus*, Groessens & Noël, pl. 2, pl. 7, fig. 26.
- 1977 *Gnathodus symmutatus homopunctatus*, Perret, pl. 51, fig. 25.
- 1978 *Gnathodus homopunctatus*, Menéndez-Álvarez, pl. 1, fig. 6.
- p 1978 *Gnathodus symmutatus*, Kozitskaya *et al.*, pl. 11, fig. 5.
- 1978 *Gnathodus homopunctatus*, Kozitskaya *et al.*, pl. 11, figs 6–7.
- 1979 *Gnathodus commutatus homopunctatus*, Buchroithner, pl. 1, fig. 3; pl. 2, fig. 1.
- 1980 *Gnathodus homopunctatus*, Metcalfe, pl. 13, fig. 17.
- 1980 *Gnathodus homopunctatus*, Tynan, pl. 1, figs 1–2.
- 1980 *Paragnathodus commutatus*, Tynan, pl. 1, figs 3–4.
- p 1981 *Gnathodus homopunctatus*, Metcalfe, p. 27, pl. 5, figs 1, 3–5 (only).
- 1982 *Gnathodus homopunctatus*, Higgins & Wagner-Gentis, pl. 34, fig. 7.
- 1984 *Gnathodus homopunctatus*, Austin & Davies, pl. 3, figs 25, 33.
- 1984 *Gnathodus homopunctatus*, Chaplin, pl. 5, figs 5–7.
- ? 1984 *Gnathodus nodosus* Bischoff, Chaplin, pl. 6, fig. 1.
- 1985 *Gnathodus homopunctatus*, Varker & Sevastopulo, p. 200, pl. 5.5, figs 14–15, 19, 21–22.
- 1985 *Gnathodus homopunctatus*, Belka, pl. 5, figs 6–14.
- 1985 *Gnathodus mermaidus* (Austin & Husri), Belka, pl. 7, fig. 9.
- 1985 *Gnathodus symmutatus* → *G. homopunctatus*, Belka, pl. 15, fig. 8.
- 1985 *Paragnathodus homopunctatus*, Weyant, pl. 5, figs 8–9.
- p 1986 *Gnathodus symmutatus*, Belka & Groessens, pl. 7, fig. 7 (only).
- 1986 *Gnathodus* cf. *homopunctatus*, Belka & Groessens, pl. 7, figs 8–10.
- 1986 *Gnathodus homopunctatus*, Belka & Groessens, pl. 7, figs 11–15.
- 1987 *Gnathodus* sp. cf. *G. homopunctatus*, Austin, pl. 13.1, figs 1–3, 12; pl. 13.2, figs 4–6, 15, 21–26; pl. 13.3, figs 4–6, 8, 10.
- p 1987 *Paragnathodus* (?) *homopunctatus*, Barskov *et al.*, pl. 16, figs 3–5 (only).
- 1987 *Gnathodus?* *homopunctatus*, Orchard, pl. 78.1, fig. 8.
- 1991 *Gnathodus* sensu lato *homopunctatus*, Stone, p. 28–29, pl. 3, figs 1–4.
- p 1993 *Pseudognathodus homopunctatus*, Perret, p. 349, 351, figs 122A, C; pl. C5, figs 21–24, 26 (only).
- 1994 *Pseudognathodus homopunctatus*, Perret *et al.*, pl. 3, fig. 14.
- 1996 *Paragnathodus homopunctatus*, Kozitskaya & Nemirovskaya in Einor *et al.*, pl. 8, fig. 20.
- 1996 *Pseudognathodus homopunctatus*, Skompski, pl. 1, fig. 10; pl. 2, fig. 3.
- 1998 «*Gnathodus*» *homopunctatus*, Belka & Lehmann, pl. 2, figs 7–8.
- p 1998 *Pseudognathodus homopunctatus*, Perri & Spalletta, pl. 2, figs 6–7 (only).
- 1999 *Pseudognathodus homopunctatus*, Meischner & Nemyrovskaya, pl. 4, figs 5, 7, 11, 23.
- 1999 *Gnathodus homopunctatus*, Somerville & Somerville, pl. 1, fig. 11.
- 2003 *Pseudognathodus homopunctatus*, Groves *et al.*, fig. 3.5a–c.



2004 *Gnathodus homopunctatus*, Bermúdez-Rochas *et al.*, p. 49–50, 52, pl. 7, figs 1–6, 8–9, 11.

2004 *Paragnathodus homopunctatus*, Tian & Coen, pl. 1, figs 17–19.

v 2005 *Pseudognathodus homopunctatus*, Blanco-Ferrera *et al.*, pl. 6.31.

2005 *Pseudognathodus homopunctatus*, Nemyrovska, p. 45–46, pl. 7, figs 2–3.

2005 *Pseudognathodus mermaidus* (Austin & Husri), Nemyrovska, p. 45–46, pl. 7, fig. 1.

2005 *Pseudognathodus homopunctatus*, Qi & Wang, pl. 1, fig. 1.

2006 *Pseudognathodus homopunctatus*, Nemyrovska *et al.*, pl. 4, figs 1–5, 7.

2006 *Gnathodus homopunctatus?*, Dumoulin *et al.*, pl. 2, fig. 13.

2009 *Paragnathodus homopunctatus*, Nikolaeva *et al.*, pl. 3.10.

2010 *Pseudognathodus homopunctatus*, Pazukhin *et al.*, pl. 3, fig. 10.

2010 *Paragnathodus homopunctatus*, Nigmadhaznov *et al.*, pl. 2, figs 4–5.

2014 *Pseudognathodus homopunctatus*, Gatovskii & Zhorina, figs 6–10.

2014 *Pseudognathodus homopunctatus*, Qi *et al.*, fig. 4m.

2016 *Pseudognathodus homopunctatus*, Kabanov *et al.*, fig. 12B.

Synonymy lists are annotated using the symbols recommended by Matthews (1973). Records preceded by (*) provide the original definition and illustration of material type and diagnosis of the species; (?) indicates doubt that the published material is within the species; (v) *vide* marks that the authors have seen the specimen/s; (p) *pars* notes that only part of the specimens in the reference belong to the species; (*non*) shows distinct identification.

Material. About 544 specimens from samples in the Austin Collection housed in the NHMUK, London. Sixty

elements from sample CLP-6 in the Alba Formation at Las Portillas del río Nevandi section (Spain; see location in Sanz-López *et al.*, 2018).

Remarks. Variation in P1 element ornamentation is associated with element size in ontogenetic series according to Gatovskii & Zhorina (2014). Four morphotypes may be differentiated. A few nodes located on each side of the cup join to form a row of nodes in the typical morphotype (Figs 2a–2b, 2e, 2j–2l). Another morphotype shows short transverse ridges instead of nodes (Figs 2c, 2f, 2m). The ridges are higher at the middle part of the row, where they are laterally displaced with respect to other ridges or nodes of the row (Figs 2c, 2e, 2h, 2i). The two rows of ridges taper to the dorsal carina where isolated nodes form a V that opens to the lower ventral part of the cup. This morphotype was described as *Gnathodus cf. homopunctatus* by Belka & Groessens (1986) and occurs together with the typical morphotype from the lowermost Viséan beds in Belgium. The ridges are normally well developed in large specimens (Figs 2i, 2m). A third morphotype shows a wide veil and a swollen area limited to the proximal ventral cup (Fig. 2d). A fourth morphotype differs by the occurrence of two rows of nodes developed on one side of the cup (Figs 3g1–3g2). All four morphotypes are observed together in the earliest Viséan sample CLP-6 from the Cantabrian Mountains.

Occurrence. *Pseudognathodus homopunctatus* first occurs just above the base of the Viséan in Belgium, the British Isles and China (Conil *et al.*, 1989; Devuyt *et al.*, 2003; Poty *et al.*, 2006). *Pseudognathodus homopunctatus* is a widely distributed species that is used to define the *Ps. homopunctatus* Zone (Higgins, 1985) in England, a local-range zone (Metcalf, 1981), or an assemblage zone (Varker & Sevastopulo, 1985), and a subzone in Belgium (Groessens, 1975). The last occurrence is in the Serpukhovian, Pendleian Regional Stage in England (Higgins, 1985). It has been reported from Europe, northern Africa, Moscow Basin, South Urals, central Asia and China (Qi & Wang, 2005; Nemyrovska *et al.*, 2006; Nikolaeva *et al.*, 2009; Nigmadhaznov *et al.*, 2010; Kabanov *et al.*, 2016; among others).

In North America, *Ps. homopunctatus* occurs in the Meramecian beds (middle Viséan) of the Saint Louis Limestone in Kansas and the Thalequah Limestone in Oklahoma (Thompson & Goebel, 1969; Godwin *et al.*,

Figure 2. (a–m) *Pseudognathodus homopunctatus* (Ziegler). **a1–a2)** Specimen NHMUK PM X 3955). **b1–b2)** NHMUK PM X 3978. **(c1–c2)** NHMUK PM X 3950 from sample Cl. 12A, Island Slumped Series in Countie Clare (Ireland). **d)** Specimen (NHMUK PM X 3915 from sample 2b, Caninia Beds, Arundian of Flintshire (North Wales) in Aldridge *et al.* (1968). **e)** Specimen NHMUK PM X 3940. **f1–f2)** Specimen NHMUK PM X 3943. **g1–g2)** NHMUK PM X 3941. **h)** NHMUK PM X 3951. **i1–i2)** NHMUK PM X 3944 from sample L. 7. **j–m)** Specimens DGO 15601–DGO 15604 from sample CLP-6 of the Alba Formation at the las Portillas de río Nevandi section, Spain. **n1–n2)** *Pseudognathodus symmutatus* (Rhodes *et al.*), re-illustrations of holotype NHMUK PM X 134, sample 3D 10 from North Crop (South Wales).

2010). It was described from the basal Chesterian beds (upper Viséan) in the Chainman Formation in Nevada and Utah (Sandberg *et al.*, 1980; Tynan, 1980) and from equivalent or younger beds in California (Stevens *et al.*, 1996), Virginia (Chaplin, 1984) and British Columbia (Orchard, 1987; Beatty, 2002). A probable late Osagean (early Viséan) occurrence was reported from Alaska (Dumoulin *et al.*, 2006).

Pseudognathodus lineatus (Austin & Husri, 1975)
(Figs 1c, 3a–3e2, 4f1–4h)

v 1975 *Gnathodus commutatus lineatus*, Austin & Husri, p. 52–53, pl. 2, figs 9a–9b; pl. 4, figs 11a–11c.

v * 1975 *Gnathodus commutatus multinodosus* Higgins, Austin & Husri, pl. 2, figs 13a–13c.

Material. About 61 specimens from ten samples (B.S. 8, Cl. 3, Cl. 9, Cl. 10, Cl. 11, Cl. 12A, Cl. 12B, Cl. 13, L. 7 and L. 9) in the Austin Collection at NHMUK.

Type material. The holotype (NHMUK PM X 1723) and paratype (NHMUK PM X 1724) previously designated by Austin & Husri (1975).

Type locality. Sample Cl. 12B, Inishtubrid Beds in the islands of the Shannon Estuary, County Clare, Ireland (see Austin & Husri, 1975).

Revised diagnosis. P1 element shows a sub-triangular cup with the widest part close to the ventral margin. The central part of the cup is a high terrace supporting variable ornamentation of a few nodes, a single row of nodes on each side of the carina, which may be replaced by an elongate belt of small nodes. Blade is high in the central part of the carina-blade and is decreasing in height towards the dorsal and ventral ends.

Description. The cup is as long as wide, sub-triangular to sub-rhombic in shape, and sub-circular in smaller specimens. It shows a proximal, central and high terrace bordered by a flared marginal area. Ornamentation is concentrated towards the margin of the terrace, away from the carina. It consists of nodes or short ridges in immature specimens, usually a single row of nodes on each side of the carina, or rarely an elongate belt of small nodes at the margins of the terrace and only a row of nodes at the dorsal termination.

Remarks. Specimens with cups of sub-circular outline in *Ps. lineatus* are morphologically close to elongated elements of *Ps. homopunctatus*, because a row of nodes or short ridges may be present in both. The blade in both taxa is identical, but the occurrence of the terrace bordered

by a veil is characteristic of *Ps. lineatus*. In our opinion, many elements identified as *G. c. lineatus* in the slides of the Austin Collection belong to *Ps. homopunctatus*. A strongly ornamented row of nodes is present in mature elements of *Ps. homopunctatus*.

The holotype of *Ps. lineatus* Austin & Husri (1975, pl. 2, fig. 9) was smaller than that of *Ps. mermaidus* (pl. 4, fig. 10), and showed poorly developed ornamentation in two short rows (compare Fig. 4f1 and Fig. 4c1). Specimens identified in slides of the Austin collection with the label *Gnathodus commutatus lineatus* are *Ps. mermaidus*, because mineral overgrowth obscured the irregular distribution of small nodes. This can only be seen under the SEM.

The element illustrated as paratype (Austin & Husri, 1975, pl. 4, figs 11a, 11b) is close to *Ps. homopunctatus*, and is differentiated by the sub-rhomboidal outline of the cup and the ornamentation of two short and strong rows of nodes (Fig. 4g).

Pseudopolygnathus lineatus shows a longitudinally elongate cup, and not a cup expanded at the rostral and caudal sides of the blade as in ornamented specimens of *Lochriea*. The denticles of the ventral part of the blade are lower than those in the middle part of the blade.

Occurrence. In the Austin Collection, this species is only known in samples from south central Ireland (Austin & Husri, 1975). It occurs in Asbian to Brigantian samples from the Durnish, Parsonage and Corgrig Lodge formations in County Limerick; Lords Rock Limestone, Island Slumped Series and Inishtubrid Beds of the Island succession, Inch Bridge limestones, Ballycorick Chert and Reef of the mainland succession in County Clare.

Pseudognathodus mermaidus (Austin & Husri, 1975)
(Figs 3f1–3i2, 4c1–4d2, 5a1–5a2)

p 1967 *Gnathodus homopunctatus* Ziegler, Spassov & Filipović, pl. 8, fig. 8 (only).

v* 1975 *Gnathodus symmutatus mermaidus*, Austin & Husri, p. 54–55, pl. 2, figs 11a–11c; pl. 4, figs 10a–10c.

p 1987 *Paragnathodus* (?) *homopunctatus*, Barskov *et al.*, pl. 16, fig. 6 (only).

1991 *Gnathodus sensu lato mermaidus*, Stone, p. 29, pl. 3, figs 5, 6.

p 1993 *Pseudognathodus homopunctatus*, Perret, p. 349, 351, fig. 122C; pl. C5, fig. 25 (only).

p 1998 *Pseudognathodus homopunctatus*, Perri & Spalletta, pl. 2, fig. 13 (only).

1999 *Pseudognathodus mermaidus*, Meischner & Nemyrovskaya, pl. 4, figs 1–3.

2012 *Lochriea homopunctatus*, Atakul-Özdemir *et al.*, p. 1288, figs 2A?, B?, C–G.

Material. About 66 specimens from nine samples in the Austin Collection, NHMUK (Cl. 3, Cl. 5, Cl. 10, Cl. 11, Cl. 12A, Cl. 12B, L. 5, L. 7, and L. 10).

Type Material. The holotype and paratype of *G. symmutatus mermaidus* are lost. The holotype of *Ps. mermaidus* (NHMUK PM X 1755) was from sample Cl. 5 in the Mermaid Beds (Inishloe Island) of County Clare, Ireland (not Cl. 15 as reported by Austin & Husri, 1975, p. 54). The paratype (NHMUK PM X 1754) came from sample Cl. 12B in the Inishtubrid Beds of the Islands in the Shannon Estuary (Austin & Husri, 1975).

Remarks. The well-developed platform shows a curved oral outline, as in other species of *Pseudognathodus*, but ornamentation consists of many small nodes on the oral surface on both rostral and caudal sides. Several authors accepted the species (Belka, 1985; Stone, 1991; Meischner & Nemyrovska, 1999), whereas others included it in the variation of *Ps. homopunctatus* (Metcalf, 1981; Perret, 1993). In our opinion, a significant characteristic is the thickening of the cup that rises as a terrace above the veil. The ornamentation is concentrated on the proximal cup adjacent to the blade, whereas the margins of the cup are smooth. Nodes can be fused into irregular lines except in the dorsal part, where they tend to be arranged in two rows displaying an acute angle with the carina.

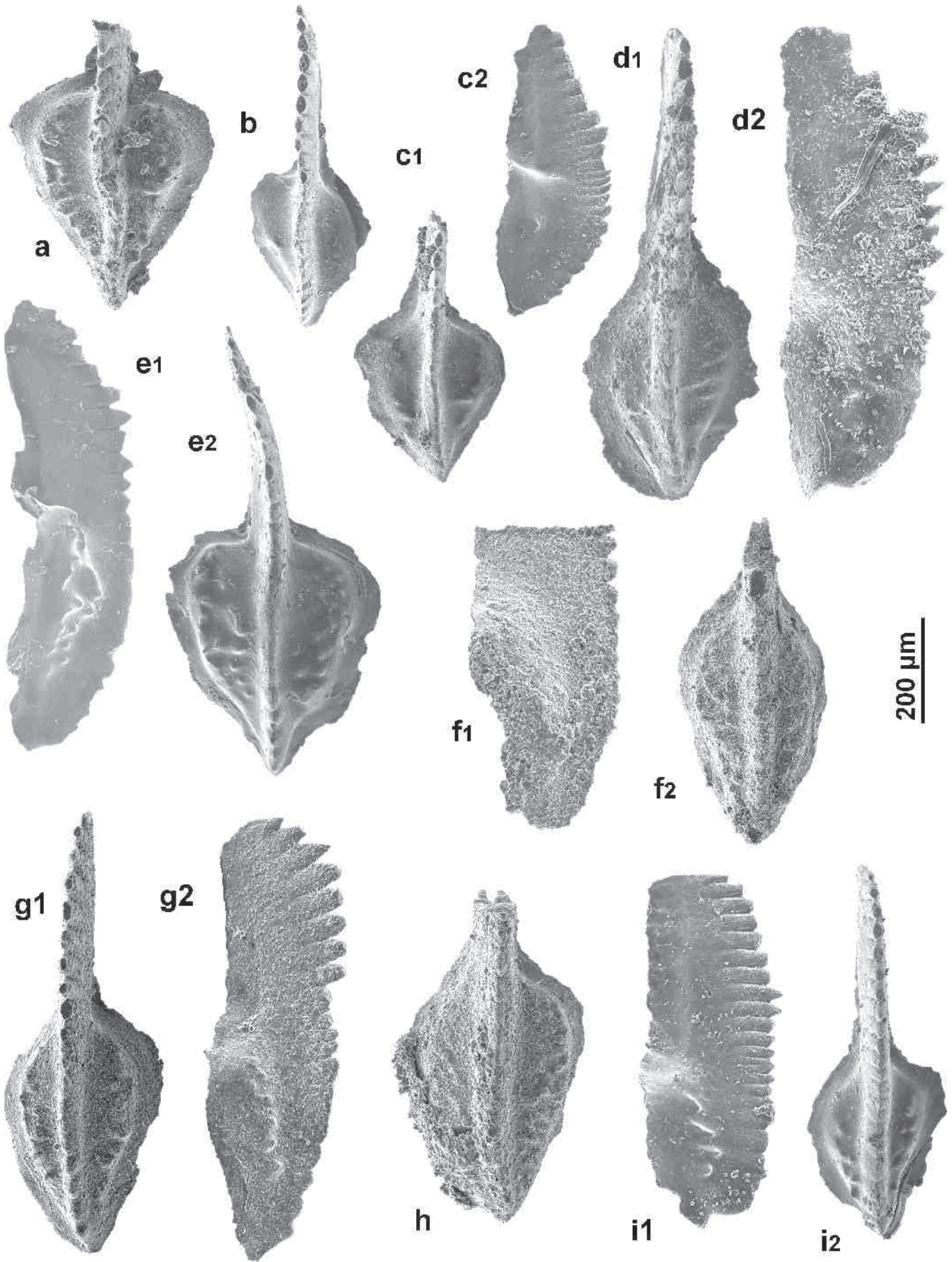
We consider that a small number of the specimens classified as *Ps. mermaidus* by Austin & Husri (1975) correspond to specimens of *Ps. homopunctatus* with overgrowths of apatite crystals observed under high magnification (samples B.S. 10 and B.S. 11 from the upper beds of the Rathkeale Formation at Durnish Point; samples L. 12a and L. 12b in the Shanagolden Formation, County Limerick; sample Cl. 5 in the Mermaid Beds in County Clare). Under the light microscope, the apatite crystals appear similar to irregularly distributed nodes. We were not able to identify any specimen of *Ps. mermaidus* in slide labelled “G. multi?, G. symm and G. homo” from sample Cl. 5, despite the table in Austin & Husri (1975, fig. 18) suggesting that two specimens and the holotype of *G. s. mermaidus* were present in sample Cl. 5. Typical specimen NHMUK PM X 3953 was taken from sample Cl. 12B that was the original sample of the lost paratype (Figs. 3i1 and 3i2). Other typical specimens were selected from sample L. 7 (NHMUK PM X 3946 and NHMUK PM X 3942; Figs 3f and 3h) from the Parsonage Formation near Corgrig Lodge, County Limerick.

The ontogenetic series of the P1 element illustrated by Atakul-Özdemir *et al.* (2012) shows small elements with *Ps. homopunctatus* morphology together with large

(mature) elements of *Ps. mermaidus*. This suggests that *Ps. mermaidus* was derived from *Ps. homopunctatus*. Identification of *Ps. mermaidus* requires large elements, because immature specimens can not be differentiated from *Ps. homopunctatus*.

Occurrence. Stone (1991) indicated the *Ps. mermaidus* ranges between the Arundian and the Asbian English substages (Viséan) on basis of the distribution described by Austin & Husri (1975). However, this distribution should be revised following our study of the assemblage slides of Austin & Husri (1975). *Pseudognathodus mermaidus* was found in the Shanagolden Limestones and the Corgrig Lodge Beds. The holotype of *Ps. mermaidus* comes from sample Cl. 5 in the Mermaid Beds (Inishloe Island, Ireland). The assemblage slide for sample Cl. 5 (NHMUK PM X 2170) only has the annotation “G. multi?” (probably meaning “*G. c. multinodosus*”), but no indication that *Ps. mermaidus* is present. We were not able to find an additional couple of elements in this slide. Austin & Husri (1975, fig. 18) suggested that *Ps. mermaidus* specimens should be present but only *Ps. homopunctatus* was found in the slide. Consequently, an early and rare occurrence of *Ps. mermaidus* in lower Viséan beds in the Shannon islands is concluded on basis of one element (the holotype). The upper beds of the Rathkeale Beds at the Durnish Point (County Limerick) and the Shanagolden Limestone in the Shanagolden area (samples L. 12a and L. 12b) contain a few doubtful elements here identified as *Ps. homopunctatus*. *Pseudognathodus mermaidus* occurs in the Durnish Limestone (samples L. 5 and B.S. 8, Austin & Husri, 1975, figs 8 and 14) with *Lochriea saharae* and above the occurrence of *L. cf. commutata* (sample L. 2). It is also present in the Shanagolden, Parsonage and Corgrig Lodge formations near Corgrig Lodge (Austin & Husri, 1975, fig. 14). In Clare County, it is rare in the upper Lords Rock Limestone, but occurs in the Island Slumped Series and the Inishtubrid beds, where it co-occurs with the upper Viséan *Lochriea nodosa* of the Shannon Basin (sample Cl. 12B).

Specimens of *Ps. mermaidus* from the Hodder Mudstone Formation, in the Craven Basin (England), were assigned to the Arundian (lower Viséan) by Atakul-Özdemir *et al.* (2012). Typical elements occur in the middle Viséan *Gnathodus prae bilineatus* Zone above the first occurrence of *L. commutata* and in the *Entogonites nasutus* Ammonoid Zone, below the first occurrence of *Gnathodus romulus* in the Rhenish Mountains, Germany (Meischner & Nemyrovska, 1999). Specimens here considered as *Ps. mermaidus* were illustrated from the Cantabrian Mountains, the Carnic Alps, Serbia and the Russian Platform (Spassov & Filipović, 1967; Park, 1983, pl. 4, fig. 33; Barskov *et al.*, 1987; Perri & Spalletta, 1998). Consequently, we suggest *Ps. mermaidus* ranges from the Arundian to the Brigantian (early Viséan to early Serpukhovian).



Pseudognathodus posadachaconae sp. nov.
(Figs 4e, 5b1–5e2)

v 1968 *Gnathodus symmutatus* Rhodes *et al.*, Aldridge *et al.*, table 1.

p v1968 *Gnathodus commutatus* (Branson & Mehl), Aldridge *et al.*, table 1.

p v1968 *Gnathodus homopunctatus* (Ziegler), Aldridge *et al.*, table 1.

p 1981 *Gnathodus homopunctatus*, Metcalfe, p. 27, pl. 5, fig. 2 (only).

Derivatio nominis. Named after Luis C. Sánchez de Posada and M. Luisa Martínez Chacón for their palaeontological contributions to knowledge of the Cantabrian Mountains.

Material. Specimens from the *Cyathaxonia* Beds in Flintshire (North Wales), 55 elements from samples 4Aa to 4Ac, 4Ba, 4Bb, 4Bd and 4Be in Aldridge *et al.* (1968).

Holotype and paratype. Holotype NHMUK PM X 3784 and paratype NHMUK PM X 3857 (Figs 5b1–5c2).

Type locality. Sample 4Ac studied by Aldridge *et al.* (1968) from the lower part of the Prestatyn Limestone, Flintshire, North Wales.

Diagnosis. Elements with a dorsal carina forming a curve and high outline in lateral view, which may be twice the height of the denticles of the ventral blade. The denticles of the dorsal carina are fused in a ridge, and the dorsal margin is high and straight. Oval cup occupies less than half the length of the element and is smooth or bears a few small, rounded nodes on either sides of the carina.

Description. Mature specimens with blade and carina that consists of 20–23 denticles. Denticles are tall and discrete on the blade but more fused at the dorsal carina, except their isolated triangular tips. Large specimens have more fused dorsal denticles. The blade is high, decreasing in height at the ventral end. The carina is up to twice the height on the fixed blade than on the free blade. A wall or high palisade is developed in the half where the basal cavity is expanded. The oral margin is curved, particularly in the fused half of the carina and decreases in height to

the dorsal end. The dorsal end is high and at right angle to the longitudinal plane of the specimen. In lateral view, the outline may be straight or concave outward, with a slightly protruding end of the carina. The cup is moderately wide and its length is less than half the length of the element. The cup is smooth or develops a short, narrow step adjacent to each side of the carina in the dorsal region. These steps may be smooth, with one small, rounded node only on one side, or two to three nodes on either side of the element. The nodes also occur in small specimens.

Remarks. The tall and well-developed dorsal carina differentiates this species from *Ps. symmutatus*, whose denticles in the dorsal carina are isolated and decrease in height toward the dorsal end. The cup is shorter and better developed than in *Ps. symmutatus*. Immature specimens of *Ps. homopunctatus* may be confused with this new species as there are a few nodes developed on the cup. However, the nodes are smaller in mature elements of *Ps. posadachaconae* sp. nov., and the denticulation and height of the carina is clearly different. We suggest this new species could be derived from *Ps. homopunctatus* through the loss of ornamentation and a smaller cup with a strong carina.

Occurrence. Metcalfe (1981) included this morphotype in *Ps. homopunctatus* from the upper Holkerian beds at the top of the Cephalopod Shales at Ings Beck (Craven Basin, England). Specimens from the *Cyathaxonia* Beds in Flintshire (North Wales) described by Aldridge *et al.* (1968) correspond to the lower part of the Prestatyn Limestone, developed basinal to the “knoll-reef” in the Asbian Loggerheads Limestone (Somerville *et al.*, 1986; Davies *et al.*, 2011). *Pseudognathodus posadachaconae* sp. nov. occurs with other shallow-water dwellers such as *Hindeodus cristula* (Youngquist & Miller), *Mestognathus beckmanni* Bischoff, *Synclydagnathus geminus* (Hinde), and together with a few elements of *Gnathodus pseudosemiglaber* Thompson & Fellows, *Lochriea saharae* Nemyrovska *et al.* and *Vogelgnathus campbelli* Rexroad. Sample 4Ae included fragments of probable *L. commutata* (Branson & Mehl) and two elements of *Vogelgnathus pesaquidi* Purnell & von Bitter.

Pseudognathodus symmutatus (Rhodes, Austin & Druce, 1969)
(Figs 1a, 2n1–2n2, 4a1–4a2)

Figure 3. a–e) *Pseudognathodus lineatus* (Austin & Husri). **(a)** Specimen NHMUK PM X 3947 from sample Cl. 12A. **(b)** Specimens NHMUK PM X 3954, **(c1–c2)** NHMUK PM X 3952. **(d1–d2)** NHMUK PM X 3938. **(e1–e2)** NHMUK PM X 1725 from sample Cl. 12B. **f–i) *Pseudognathodus mermaidus*** (Austin & Husri). **f1–f2)** Specimen NHMUK PM X 3946 from sample L. 7. **g1–g2)** Specimen NHMUK PM X 3939, sample L. 7. **h)** Specimen NHMUK PM X 3942, sample L. 7. **i1–i2)** Specimen NHMUK PM X 3953 from sample Cl. 12B.

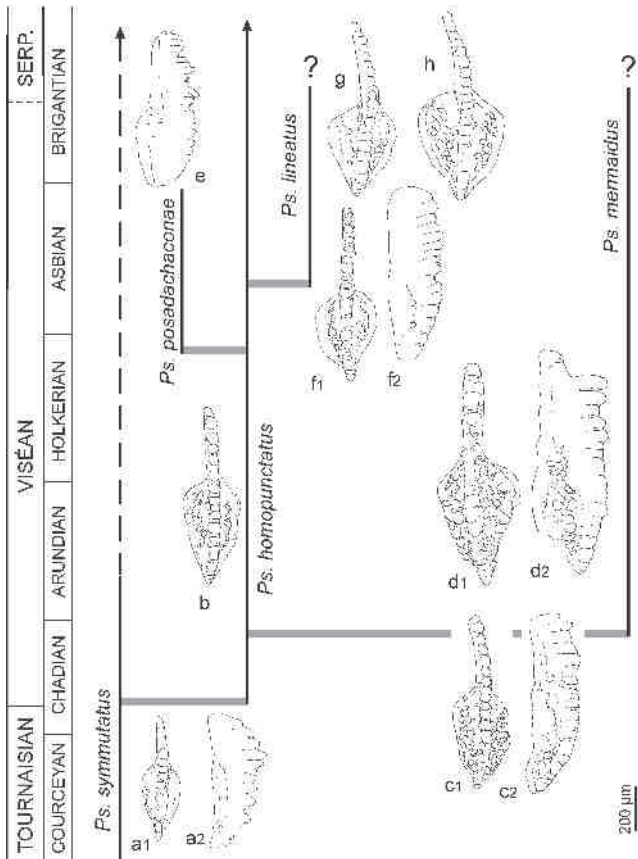


Figure 4. Proposed phylogeny of *Pseudognathodus* species based on the morphology of the P1 element and stratigraphic ranges plotted against British Regional stages for the upper Tournaisian and Viséan. **a1–a2)** *Pseudognathodus symmutatus* (Rhodes *et al.*), NHMUK PM X 1750, sample L. 7. **b)** *Pseudognathodus homopunctatus* (Ziegler), NHMUK PM X 1753, sample Cl. 5. **c1–d2)** *Pseudognathodus mermaidus* (Austin & Husri), holotype NHMUK PM X 1755 and paratype NHMUK PM X 1754. **e)** *Pseudognathodus posadachaconae* sp. nov., paratype NHMUK PM X 3857. **f–h)** *Pseudognathodus lineatus* (Austin & Husri), sample Cl. 12B. **(f1–f2)** Holotype NHMUK PM X 1723. **(g)** Paratype NHMUK PM X 1724. **(h)** Specimen NHMUK PM X 1725.

? * v 1969 *Gnathodus symmutatus*, Rhodes *et al.*, 108, pl. 19, figs 1a–4c.

p v 1975 *Gnathodus symmutatus symmutatus*, Austin & Husri, pl. 4, figs 7a–7c (only).

non1975 *Gnathodus symmutatus*, Higgins, p. 34, pl. 10, figs 8–9 [= *Lochriea commutata* (Branson & Mehl)].

1976 *Gnathodus symmutatus*, Groessens in Conil *et al.*, pl. 6, fig. 19.

1977 *Gnathodus symmutatus symmutatus*, Perret, pl. 1, fig. 24.

p? 1978 *Gnathodus symmutatus*, Kozitskaya *et al.*, pl. 11, fig. 4 (only)

non1987 *Paragnathodus* (?) *symmutatus*, Barskov *et al.*, pl. 16, figs 1–2 (= *Lochriea commutata*).

1991 *Gnathodus* sensu lato *symmutatus*, Stone, p. 29–30, pl. 3, figs 7–9.

1993 *Pseudognathodus symmutatus*, Perret, p. 351, fig. 122B (1).

1996 *Paragnathodus symmutatus*, Vorontzova in Einor *et al.*, pl. 42, fig. 28.

non 1999 *Pseudopolygnathus symmutatus*, Meischner & Nemyrovskaya, pl. 4, fig. 6 (= *Lochriea commutata*).

Material. Holotype (NHMUK PM X 134), paratypes (NHMUK PM X 135, NHMUK PM X 136), 38 specimens from samples CYD 7 to 3D 14/15 from North Crop (South Wales), material studied by Rhodes *et al.* (1969) and about 100 specimens from Austin & Husri (1975).

Type locality. Sample 3D 10 from Mellte Bridge, at the confluence of the rivers Mellte and Sychryd near Craig-y-Dinas, in North Crop (South Wales), according to Rhodes *et al.* (1969).

Revised diagnosis. Element with a convex oral outline of a slightly expanded cup tapers at both ends. Ornamentation is lacking or a small node (rarely two) is located on the cup. Blade with high denticles, except the lower at the ventral portion. The dorsal carina shows denticles decreasing in height.

Remarks. The original diagnosis indicated that *Ps. symmutatus* has a small, unornamented cup (Rhodes *et al.*, 1969). Stone (1991) suggested that it is not possible to differentiate immature specimens of *Ps. homopunctatus* from *Ps. symmutatus*. This is illustrated by the type material designed by Rhodes *et al.* (1969; compare pl. 19, figs 1–4 with figs 5–8). These are small, probably immature elements, and occur with larger specimens assigned to *Ps. homopunctatus* in the same samples. The holotype NHMUK PM X 134 (sample 3D 10) has a small node in the rostral part of the cup and the paratype, NHMUK PM X 135, from the same sample a small indentation. The latter is the smallest of the observed type specimens. Paratype NHMUK PM X 136 (sample 3d 14/15) has a small node on the caudal part of the cup. Perret (1993) included specimens with a small node in *Ps. symmutatus*, which she considered transitional to *Ps. homopunctatus*.

Minute P1 elements with *Ps. symmutatus* morphology and without node or indentation, are interpreted as a very early stage in the growth of *Ps. homopunctatus* in samples studied by us from the Cantabrian Mountains and the

Pyrenees. This conclusion is based on a full ontogenetic series showing a range of sizes, and the progressive development of ornamentation. However, large specimens assigned to *Ps. symmutatus* seem to be illustrated from Belgium by Conil *et al.* (1976) and a detailed description of this material needs to be undertaken. The mature elements studied by Austin & Husri (1975), Stone (1991) and Perret (1993) show a smooth cup which occupies more than half the length of the element. One or two small nodes may be present on the dorsal part of the cup. The oral denticulation of the carina consists of wide, triangular teeth that become narrower at the ventral part of the blade. The height is lower at the margins than at the central part of the blade.

Occurrence. *Pseudognathodus symmutatus* may have inhabited more onshore environment than typical *Ps. homopunctatus* according to Stone (1991). In Belgium and China, *Ps. symmutatus* has been recovered from older beds than *Ps. homopunctatus* (Conil *et al.*, 1976; Tian & Coen, 2005). It ranges from the uppermost Tournaisian to lowermost Viséan, from beds with *Scaliognathus anchoralis* and *Mestognathus praebeckmanni*, to beds at the first occurrence of *M. beckmanni* (Conil *et al.*, 1976, 1988). It was reported at the last occurrence of *S. anchoralis* in the Pyrenees (Marks & Wensink, 1970; Boersma, 1973; Perret, 1993). Further work is required to verify the status of *Ps. symmutatus* and its last occurrence in upper Viséan to Serpukhovian beds.

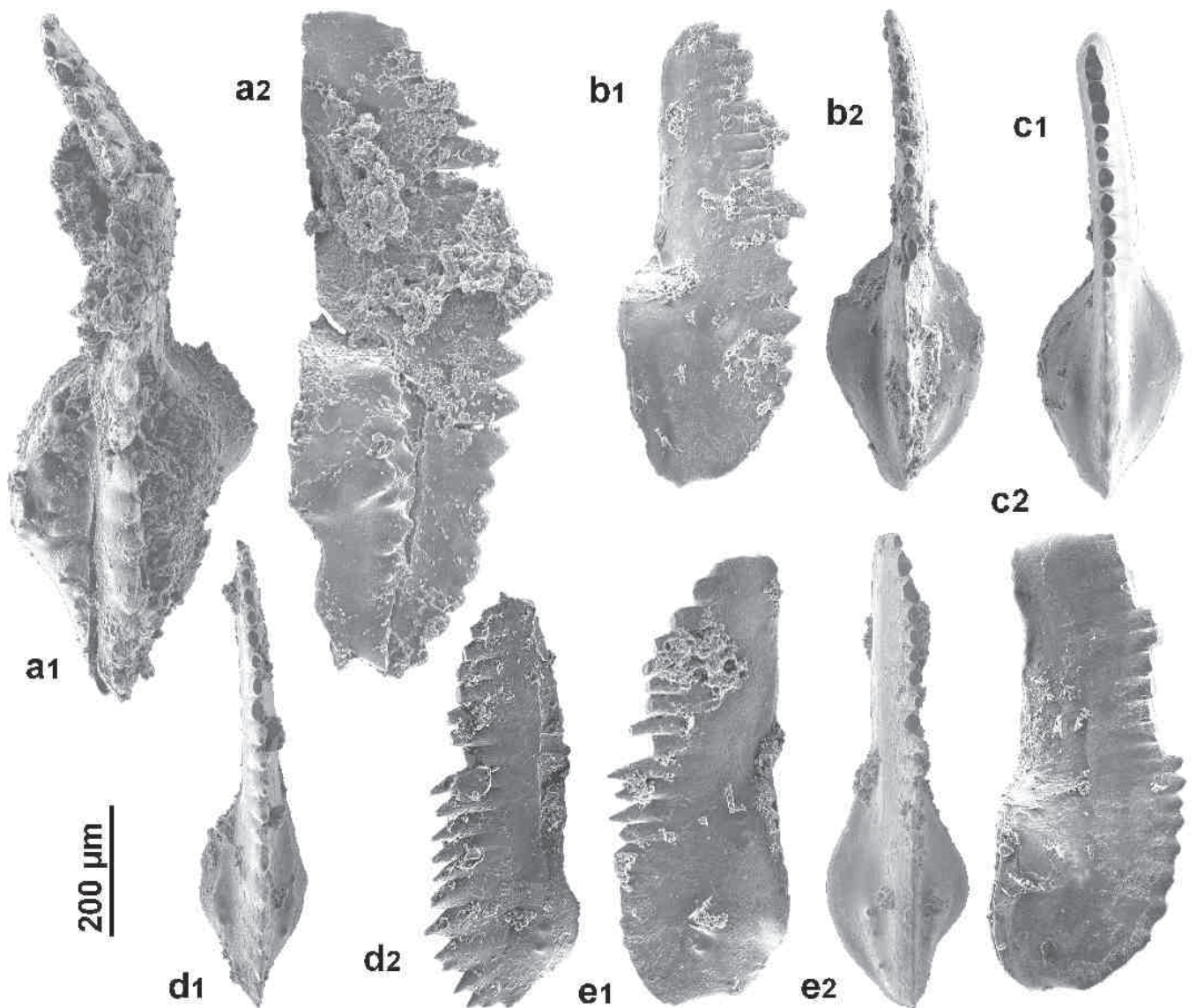


Figure 5. a1–a2) *Pseudognathodus mermaidus* Austin & Husri, specimen NHMUK PM X 3949, sample Cl. 12A. b–e) *Pseudognathodus posadachaonae* sp. nov. (b1–b2) Paratype NHMUK PM X 3857 from sample 4Ac. (c1–c2) Holotype NHMUK PM X 3784 from sample 4Ac. (d1–d2) Specimen NHMUK PM X 3866 from sample 4Ba. (e1–e2) Specimen NHMUK PM X 3865 from sample 4Ba.

4. VALIDITY AND DISTRIBUTION OF *PSEUDOGNATHODUS*

The late Tournaisian *Ps. symmutatus* is the oldest known species of *Pseudognathodus* in the stratigraphic record (Fig. 4). The origin of this species is unknown, although it is usually assumed to be derived from a species with a spathognathodid P1 element. Tian & Coen (2005) proposed a derivation from “*Spathognathodus*” *macer* Branson & Mehl, although their P1 elements are very distinct, in our opinion. *Pseudognathodus homopunctatus* evolved from *Ps. symmutatus* developing rows of nodes or short ridges in its growth. It dispersed worldwide just above the lower boundary of the Viséan (Fig. 4). *Pseudognathodus mermaidus* evolved from *Ps. homopunctatus* developing a proximal terrace ornamented by many small nodes in the lower Viséan (Arundian). *Pseudognathodus mermaidus* seems to have a moderately wide distribution in northern Europe and the Russian platform (Fig. 6). The P1 element of *Ps. posadachaconae* sp. nov. shows a high, rostral carina and a slow rate of development through ontogeny of cup and ornamentation, which may be lacking, during the growth of element. The morphology is similar to mature, large *Ps. symmutatus*, but the common occurrence of nodes in immature elements suggests a derivation from *Ps. homopunctatus*. It is known from upper Holkerian to Asbian and only in the North Wales and English Craven extensional basins (Fig. 6).

Pseudognathodus lineatus probably evolved in the Asbian (upper Viséan) from *Ps. homopunctatus* through the modification of the wide and triangular cup with a proximal terrace. The ornamentation of ridges and nodes suggests a convergent evolution with ornamented species of *Lochriea* that diversified in the Brigantian (Barham *et al.*, 2015). *Pseudognathodus lineatus* is considered to be restricted to southwestern Ireland (Fig. 6).

The last occurrence of *Pseudognathodus* seems to be in the Serpukhovian, probably in the lower part and for the wide-range and cosmopolitan species, *Ps. homopunctatus* and *Ps. symmutatus* (Figs 4, 6). However, stratigraphic ranges may be open to conjecture because differentiation of immature specimens of *Ps. symmutatus* and *Ps. homopunctatus* cannot be done without a well-preserved ontogenetic series including adult growth. There is a similar situation for immature specimens of *Ps. homopunctatus* and *Ps. mermaidus*.

The phylogeny of *Pseudognathodus* based on P1 elements shows different trends to other lineages, or clades such as the related *Protognathodus* and *Gnathodus*. This distinctive evolutionary history suggests that the genus *Pseudognathodus* is valid based on changes in the P1 element. Knowledge of the full apparatus will also help to decipher the origin and to show the relationships with other genera and families. The homeomorph genus *Protognathodus* evolved from the latest Devonian to the late Tournaisian from a smooth

cup-species to a diversely ornamented species (Lane *et al.*, 1980). During the upper Viséan and Serpukhovian, the genus *Lochriea* had more diverse and ornamented species. This time also marked the widest diversity of *Pseudognathodus* (Asbian to Brigantian). However, this diversity is known only from the British Isles and Ireland, and some species (*Ps. lineatus* and *Ps. posadachaconae* sp. nov.) seem to have been strongly restricted ecologically, with short stratigraphic ranges suggesting that they were specialist taxa. In contrast, *Ps. homopunctatus* and *Ps. symmutatus* seem to have been generalist taxa with a wide distribution from shallow-water to deep-water settings of the Palaeo-Tethys. Abundant small specimens and poorly ornamented elements occur in samples from deep-water basins, for example in Spain (Blanco-Ferrera *et al.*, 2005).

Pseudognathodus does not seem to have dispersed widely in the basins of North America (Fig. 6). Probable early Viséan (late middle Osagean) occurrences of *Ps. homopunctatus* are described only in northern Alaska (de Long Mountains) by Dumoulin *et al.* (2006) and rare occurrences have been reported from the Meramecian Regional Substage (middle Viséan) in Kansas and Oklahoma (Thompson & Goebel, 1969; Godwin *et al.*, 2010). In other North American basins, it occurred from the basal Chesterian Substage (as in Utah and California) or Chesterian beds, upper Viséan (Virginia and Quesnel Terrane of British Columbia, Canada) (Sandberg *et al.*, 1980; Tynan, 1980; Chaplin, 1984; Orchard, 1991; Beatty, 2002). The first occurrence of *Ps. homopunctatus* in Utah is notable as it is below the diverse ammonoid faunas of the Asbian (Korn & Titus, 2011), and from beds recording the first occurrence of *Gnathodus bilineatus*. Consequently, wide diversification of *Pseudognathodus* on the southern margin of the Laurussian landmass seems to be consistent with dispersion of *Pseudognathodus* in the carbonate platforms and basins of North America.

6. CONCLUSIONS

Pseudognathodus is a valid genus differentiated from other conodont genera by the morphology of the P1 element and its evolutionary history. Upper Tournaisian *Ps. symmutatus* with an unornamented cup led to *Ps. homopunctatus* and this to different ornamented species. Immature specimens are difficult to differentiate and mature elements are needed to distinguish closely related species. Diagnostic specific characteristics tend to only be developed within mid-large sized specimens. The species diversity of *Pseudognathodus* increased in the upper Viséan. Endemic *Ps. lineatus* and *Ps. posadachaconae* sp. nov. (and maybe *Ps. mermaidus*) evolved from *Ps. homopunctatus*, which was widely distributed geographically and stratigraphically.

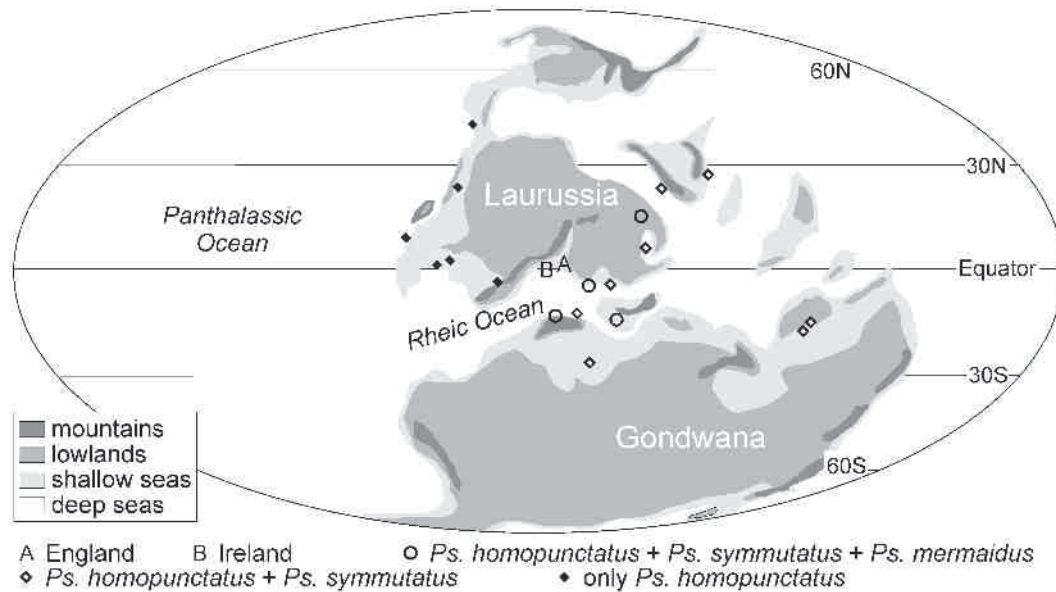


Figure 6. Viséan palaeogeography (from Rowley *et al.*, 1985) showing the distribution of *Pseudognathodus*.

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NOMENCLATURE ACT

This published work and the nomenclature acts it contains have been registered in ZooBank, the proposed online registration system for the International Code of Zoological Nomenclature. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “<http://zoobank.org/>”. The LSIDs for this publication are BF94715F-9C88-4A49-B092-29E8B48CD3EC (*Pseudognathodus* Perret, 1993), 3C12E001-AC29-49DD-8877-90DEADAE6789 (*Pseudognathodus lineatus* Austin & Husri, 1975), and FC71B345-D4F5-4CA5-A2F6-8E1C8515ECD0 (*Pseudognathodus posadachaconae* sp. nov.).

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