

Original article

Taxonomy of *Ptychagnostus atavus*: A key trilobite in
defining a global Cambrian stage boundaryTaxonomie de *Ptychagnostus atavus* : un trilobite clé pour
la définition de la limite globale du CambrienPer Ahlberg^{a,*}, Niklas Axheimer^a, Richard A. Robison^b^a Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, 22362 Lund, Sweden^b Department of Geology, University of Kansas, Lawrence, KS 66045, USA

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Abstract

The taxonomy of *Ptychagnostus atavus* (Tullberg, 1880) and *Ptychagnostus intermedius* (Tullberg, 1880) has been confused, in part at least, because of inadequate or erroneous illustrations of specimens from syntype series. From further examination and new illustrations we conclude that those series are conspecific and that *P. atavus* is the senior synonym of *P. intermedius*. Laurentian agnostoids previously assigned to *P. intermedius* are reassigned to *Ptychagnostus sinicus* Lu, 1957. As revised, *P. atavus* is a common, globally distributed species in open-marine lithofacies. Clarification of its taxonomy is important because its first appearance datum (FAD) will likely define the base of a new global Cambrian stage. © 2007 Elsevier Masson SAS. All rights reserved.

Résumé

Par le passé, des confusions ont été faites sur la taxonomie de *Ptychagnostus atavus* (Tullberg, 1880) et *Ptychagnostus intermedius* (Tullberg, 1880) engendrées en partie par une illustration inadéquate ou erronée des spécimens de la série syntypique. À partir d'études approfondies et de nouvelles illustrations nous pouvons conclure que ces séries sont conspécifiques et que *P. atavus* est le synonyme senior de *P. intermedius*. Des agnostoïdes laurentiens précédemment attribués à *P. intermedius* sont réassignés à *Ptychagnostus sinicus* Lu, 1957. Suite à cette révision, *P. atavus* est donc une espèce commune et globalement distribuée dans les lithofaciès marins ouverts. La clarification de sa taxonomie est importante parce que son niveau de première apparition sera probablement la limite globale de la base du Cambrien. © 2007 Elsevier Masson SAS. All rights reserved.

Keywords: Cambrian; Agnostida; *Ptychagnostus atavus*; Taxonomy; GSSP; Sweden

Mots clés : Cambrien ; Agnostida ; *Ptychagnostus atavus* ; Taxonomie ; GSSP ; Suède

1. Introduction

The International Subcommission on Cambrian Stratigraphy (ISCS) is working toward global subdivision of the Cambrian System into four series and ten stages (Babcock et al., 2005). The uppermost Cambrian series, Furongian, and its basal stage, Paibian, each defined by the FAD of *Glyptagnostus reticulatus* (Angelin, 1851), are the first and only Cambrian units thus far

ratified by the International Union of Geological Sciences (Peng and Babcock, 2003; Peng et al., 2004). A proposal to define the middle stage of the third Cambrian series on the FAD of *Ptychagnostus atavus* (Babcock et al., 2004) was recently approved by ISCS vote, and IUGS ratification is pending.

Originally described from the middle Cambrian of Andrarum, Scania, southern Sweden (Fig. 1), *P. atavus* has been reported from all Cambrian palaeocontinents (e.g., Robison, 1982, 1984; Rowell et al., 1982). However, opinions on its synonyms have differed, in part because of Tullberg's (1880) inadequate sketches and Westergård's (1946) retouched photographs of syntypes. The purpose of this paper is

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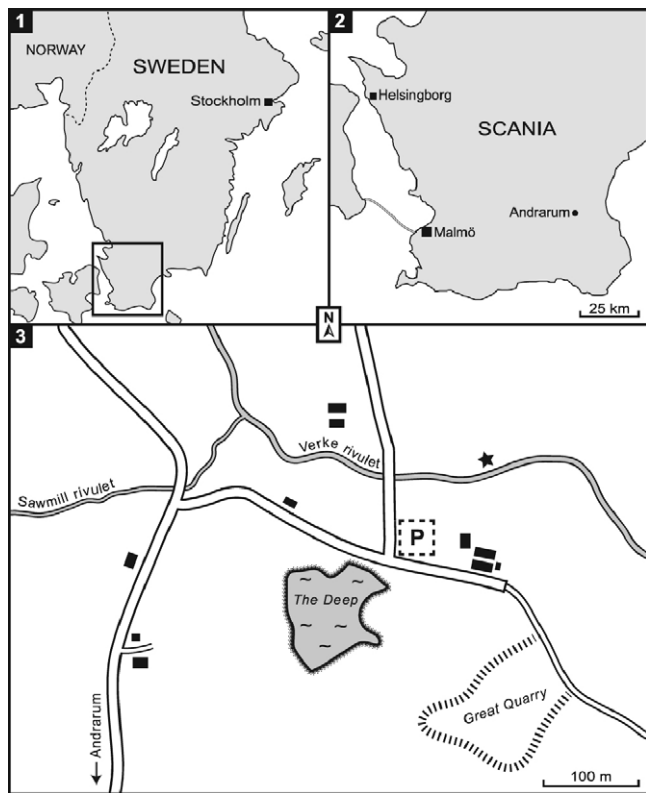


Fig. 1. 1. Orientation map of southern Scandinavia. 2. Map of Scania, southernmost Sweden, showing the location of Andrarum. 3. Map of the Andrarum area showing the type locality for “*Ptychagnostus intermedius*”, marked by an asterisk.

Fig. 1. 1. Carte du sud de la Scandinavie. 2. Carte de la Scanie, extrémité sud de la Suède, montrant la localisation d’Andrarum. 3. Carte de la région d’Andrarum montrant la localité type de « *Ptychagnostus intermedius* », marquée par un astérisque.

to clarify the concept of *P. atavus* based on examination and re-illustration of type specimens.

2. Systematic Palaeontology

Morphological terminology follows Robison (1982) and Whittington and Kelly (1997). All illustrated specimens are in the type collections of the Department of Geology, Lund University (LO).

Family PTYCHAGNOSTIDAE Kobayashi, 1939

Genus *Ptychagnostus* Jaekel, 1909

Type species: *Agnostus punctuosus* Angelin, 1851; original designation. For an official ruling on conservation of the accepted usage of *A. punctuosus* as type species, see International Commission on Zoological Nomenclature (1993).

Diagnosis: See Peng and Robison (2000).

Remarks: We follow the concept of *Ptychagnostus* discussed by Robison (1982, 1984) and Peng and Robison (2000), who listed subjective synonyms. The genus is characterised by a median preglabellar furrow, a complete axial furrow, elongate basal lobes, and usually evident pygidial F1 and F2 furrows of near equal depth. The posteroaxis is

commonly ogival, whereas the presence and numbers of spines as well as surface sculptures are variable.

Ptychagnostus is a common, globally distributed genus that ranges from the traditional lower middle Cambrian (*Ptychagnostus praecurrens* Zone) to the upper middle Cambrian (*Lejopyge laevigata* Zone of Peng and Robison, 2000).

Ptychagnostus atavus (Tullberg, 1880)

Fig. 2(1–12)

1880. *Agnostus atavus* n. sp. - Tullberg, pp. 14–15, Pl. 1, Figs. 1a–d.

1880. *Agnostus intermedius* n. sp. - Tullberg, p. 17, Pl. 1, Figs. 4a, b.

1883. *Agnostus intermedius* Tullberg - Linnarsson, p. 32.

1902. *Agnostus intermedius* Tullberg - Grönwall, p. 52.

1909. *Ptychagnostus atavus* (Tullberg) - Jaekel, p. 400.

1909. *Ptychagnostus intermedius* (Tullberg) - Jaekel, p. 400.

1929. *Agnostus intermedius* Tullberg - Strand, p. 344.

1939. *Ptychagnostus intermedius* (Tullberg) - Kobayashi, pp. 152–153.

pars 1946. *Ptychagnostus* (*Ptychagnostus*) *atavus* (Tullberg) - Westergård, pp. 76–77, Pl. 11, Figs. 8–23 (not Figs. 24, 25 = *Ptychagnostus affinis*).

1968. *Ptychagnostus* (*Ptychagnostus*) *punctuosus affinis* (Brøgger) - Palmer, p. 28, Pl. 4, Figs. 26, 27.

1979. *Ptychagnostus intermedius* (Tullberg) - Öpik, p. 95, Pl. 41, Fig. 8.

1980. *Ptychagnostus intermedius* Tullberg - Ergaliev, pp. 69–70, Pl. 1, Figs. 18–20.

1999. *Ptychagnostus atavus* (Tullberg) - Fedoseev, Pl. 2, Fig. 9.

2000. *Ptychagnostus atavus* (Tullberg) - Peng and Robison, pp. 69–70, Fig. 52 (see for much additional synonymy).

?2000. *Ptychagnostus atavus* (Tullberg) - Pegel, Fig. 11.13 (? = *P. affinis*).

2001. *Ptychagnostus atavus* (Tullberg) - Babcock and Peng, pp. 250–251.

2001. *Ptychagnostus atavus* (Tullberg) - Pham, p. 297.

2003. *Ptychagnostus atavus* (Tullberg) - Axheimer and Ahlberg, p. 147, Figs. 5B, C.

?2003. *Ptychagnostus* cf. *intermedius* (Tullberg) - Axheimer and Ahlberg, p. 147, Fig. 7A.

2005. *Ptychagnostus atavus* (Tullberg) - Peng et al., Fig. 4.1–2.

Lectotype: A nearly complete cephalon (Fig. 2(1–2); LO354T) illustrated by Tullberg (1880: Pl. 1, Figs. 1a, c); selected and re-illustrated by Westergård (1946: p. 130, Pl. 11, Fig. 8). For further discussion, see Robison (1984, p. 18).

Description of types: Lectotype cephalon about equal in maximum length and width (Table 1), and widest opposite M3. Border narrow, slightly widening toward anterior; sagittal length about five percent of total cephalic length. Posterior margin having paired fulcral processes rather than spines. Genae weakly scrobiculate but lacking paired crescentic scrobiculae opposite anterior end of glabella. Median preglabellar furrow complete, narrow, and moderately deep. Glabella tapered forward, slightly constricted at F3, and acutely

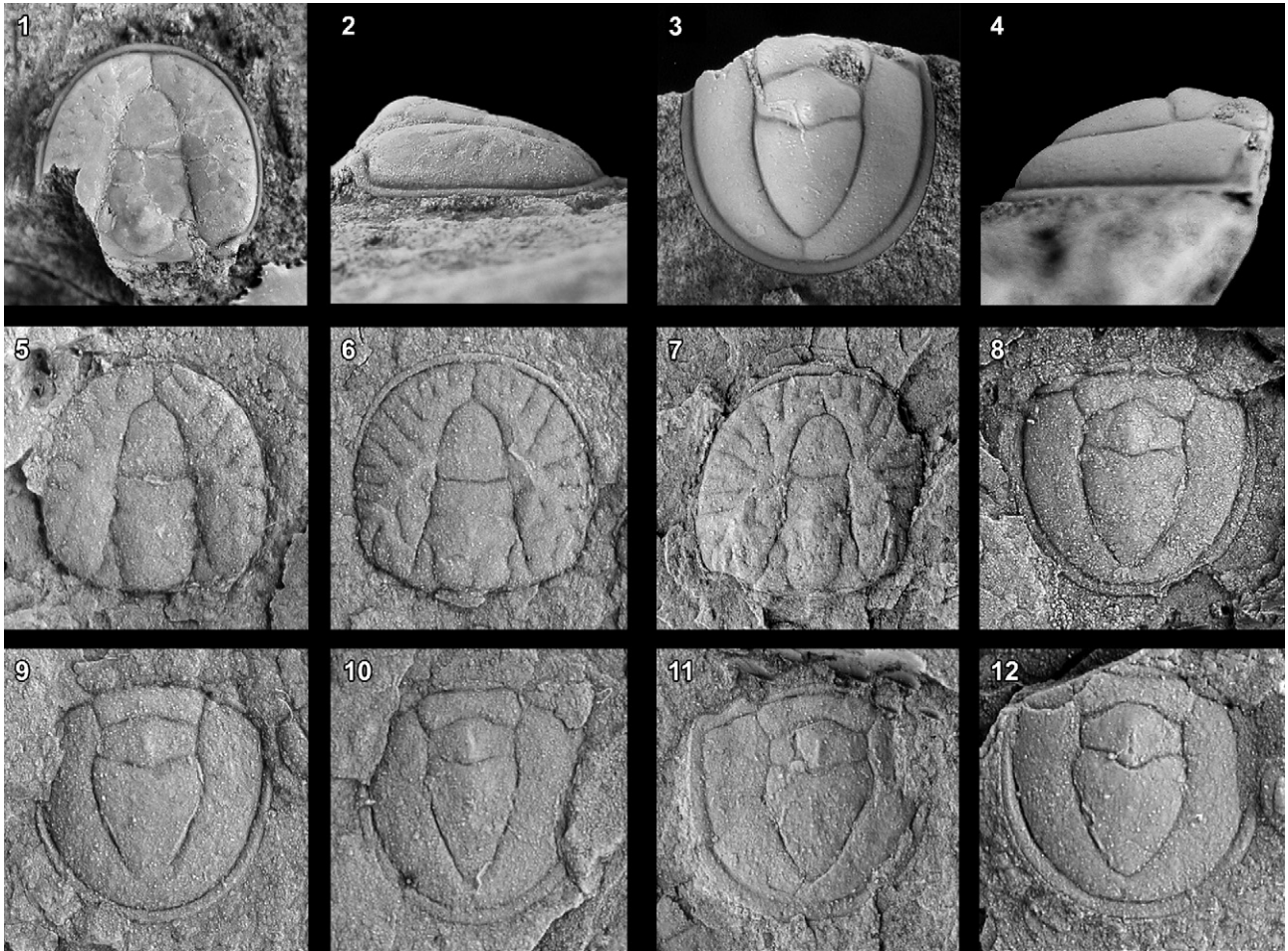


Fig. 2. *Ptychagnostus atavus* from the Andrarum area, Scania, southern Sweden. **1–4.** *P. atavus* collected from a loose stinkstone at Forsemölla. **1.** Cephalon, lectotype selected by Westergård (1946), original of Tullberg (1880: Pl. 1, Fig. 1a, c) and Westergård (1946: Pl. 11, Fig. 8), LO354T, $\times 6$. **2.** Lateral view of LO354T, $\times 7$. **3.** Pygidium, syntype, original of Tullberg (1880: Pl. 1, Fig. 1b, d) and Westergård (1946: Pl. 11, Fig. 10), LO355T, $\times 10$. **4.** Lateral view of LO355T, $\times 11$. **5–12.** *P. intermedius* (a junior synonym of *P. atavus*) collected from alum shale at an undetermined stratigraphical level at the Verke rivulet. **5.** Cephalon, lectotype selected by Ergaliev (1980), original of Westergård (1946: Pl. 11, Fig. 19), LO361T, $\times 8$. **6–12.** Syntypes. **6.** Cephalon, LO9688t, $\times 8$. **7.** Cephalon, LO9689t, $\times 7$. **8.** Pygidium, original of Westergård (1946: Pl. 11, Fig. 21), LO3432t, $\times 8$. **9.** Pygidium, LO9690t, $\times 9$. **10.** Pygidium, LO9691t, $\times 11$. **11.** Pygidium, LO9692t, $\times 8$. **12.** Pygidium, LO9693t, $\times 9$.

Fig. 2. *Ptychagnostus atavus* de la région d'Andrarum, Scanie, Suède méridionale. **1–4.** *P. atavus* récolté dans un calcaire fétide provenant de Forsemölla. **1.** Cephalon, lectotype sélectionné par Westergård (1946), original de Tullberg (1880 : Pl. 1, Fig. 1a, c) et Westergård (1946 : Pl. 11, Fig. 8), LO354T, $\times 6$. **2.** Vue latérale de LO354T, $\times 7$. **3.** Pygidium, syntype, original de Tullberg (1880 : Pl. 1, Fig. 1b, d) et Westergård (1946 : Pl. 11, Fig. 10), LO355T, $\times 10$. **4.** Vue latérale de LO355T, $\times 11$. **5–12.** *P. intermedius* (un junior synonyme de *P. atavus*) récolté dans un niveau stratigraphique indéterminé dans des ardoises, ruisseau Verke. **5.** Céphalon, lectotype sélectionné par Ergaliev (1980), original de Westergård (1946 : Pl. 11, Fig. 19), LO361T, $\times 8$. **6–12.** Syntypes. **6.** Céphalon, LO9688t, $\times 8$. **7.** Céphalon, LO9689t, $\times 7$. **8.** Pygidium, original de Westergård (1946 : Pl. 11, Fig. 21), LO3432t, $\times 8$. **9.** Pygidium, LO9690t, $\times 9$. **10.** Pygidium, LO9691t, $\times 11$. **11.** Pygidium, LO9692t, $\times 8$. **12.** Pygidium, LO9693t, $\times 9$.

rounded anteriorly; F2 weak; F3 narrow and straight. Median glabellar node is behind midpoint of M2 and slightly behind posteroglabellar midpoint. Basal lobes elongate, divided, and separated from glabella by moderately deep basal furrow.

Syntype pygidium (Fig. 2(3, 4); Tullberg, 1880: Pl. 1, Fig. 1b, d; LO355T) 1.15 times wider than long, excluding articulating half ring (Table 1). Margin lacking spines. Border uniform in width and proportionally wider than cephalic border; sagittal length about nine percent of pygidial length, excluding articulating half ring. Pleural fields smooth. Median postaxial furrow complete, narrow, and shallow. Axis slightly constricted at M2. Posteroaxis weakly ogival, 1.2 times longer than anteroaxis, and slightly convex upward in lateral profile

(Fig. 2(4)). M2 hexagonal with ovate median tubercle of moderate size distinctly indenting F2.

Remarks: *P. atavus* was initially described by Tullberg (1880) and illustrated by four sketches. The syntypes, one cephalon and one pygidium, were collected in 1876 by A.G. Nathorst from a loose stinkstone (*orsten*) at Forsemölla in the Andrarum area, Scania (locality 4 of Tullberg, 1880, and Moberg, 1910) and except for minor breakage are well preserved. One additional cephalon, illustrated by Westergård (1946: Pl. 11, Fig. 9) and reported to be associated with the syntypes, could not be located in the collections at Lund University. Tullberg (1880) thought the type-bearing stinkstone originated from a level between the Fragment Limestone and

Table 1

Dimensions (in mm) of cephalon and pygidia of *Ptychagnostus atavus*. Measurements were made with a micrometer eyepiece fitted inside a binocular microscope. All dimensions were measured as straight-line distances with an accuracy of about 0.05 mm. Lc, maximum length (sag.) of cephalon; Lcb, length (sag.) of cephalic border (including border furrow); G, length (sag.) of glabella; N, distance (sag.) from rear of glabella to highest point of median node; Wc, maximum width (tr.) of cephalon; Wg, maximum width (tr.) of glabella (excluding basal lobes); Lp₁, maximum length (sag.) of pygidium (including articulating half ring); Lp₂, length (sag.) of pygidium (excluding articulating half ring); Lpa, length (sag.) of pygidial axis (excluding articulating half ring); Lpb, length (sag.) of the posterior pygidial border (including border furrow); Wp, maximum width (tr.) of pygidium; Wpa, maximum width (tr.) of pygidial axis. Estimated measurements are denoted with a question mark.

Tableau 1

Dimensions (en mm) des cephalon et pygidia de *Ptychagnostus atavus*. Des mesures ont été faites avec un micromètre adapté dans l'oculaire d'un microscope binoculaire. Toutes les dimensions ont été mesurées comme des distances en ligne droite avec une précision de presque 0,05 mm. Lc, longueur maximale (sag.) du céphalon ; Lcb, longueur (sag.) du bord céphalique (incluant le sillon marginal antérieur) ; G, longueur (sag.) de la glabella ; N, distance (sag.) de l'arrière de la glabella jusqu'au point le plus haut du nodule moyen ; Wc, largeur maximale (tr.) du céphalon ; Wg, largeur maximale (tr.) de la glabella (excluant les lobes basales) ; Lp₁, longueur maximale (sag.) du pygidium (incluant le demi-anneau articulé) ; Lp₂, longueur (sag.) du pygidium (excluant le demi-anneau articulé) ; Lpa, longueur (sag.) du rachis (excluant le demi-anneau articulé) ; Lpb, longueur (sag.) du bord postérieur (incluant le sillon du bord) ; Wp, largeur maximale (tr.) du pygidium ; Wpa, largeur maximale (tr.) du rachis pygidial. Des mesures estimées sont marquées par un point d'interrogation.

	Lc	Lcb	G	N	Wc	Wg
<i>P. atavus</i>						
LO354T	5.00	0.25	3.55	1.00	4.80	1.70
" <i>P. intermedius</i> "						
LO361T	3.75?	—	3.15	0.80	3.70?	1.40
LO9688t	4.00	0.20	3.15	1.00	4.10	1.45
LO9689t	4.15	0.20	3.35	1.30	4.00?	1.15
	Lp ₁	Lp ₂	Lpa	Lpb	Wp	Wpa
<i>P. atavus</i>						
LO355T	—	3.25	2.90	0.30	3.75	1.55
" <i>P. intermedius</i> "						
LO3432t	4.00	3.80	3.20	0.25	4.10	1.70
LO9690t	3.80	3.50	3.00?	0.25	3.60	1.60
LO9691t	3.10	2.95	2.35	0.20	2.90?	1.13
LO9692t	3.90	3.70	3.00	0.25	4.00?	1.60?
LO9693t	3.70	3.60	2.90	0.25	3.80?	1.55

the Exsulans Limestone, an interval probably within the *P. gibbus* Zone. However, Westergård (1942: p. 17; Westergård, 1944: p. 22) showed that *P. atavus* consistently occurs at higher stratigraphic levels, and that the *P. atavus* Zone of Tullberg (1882) overlies the *P. gibbus* Zone (cf. Westergård, 1940: p. 62).

Tullberg (1880) also described the new species *A. intermedius*, which he noted to be morphologically similar to both *Agnostus affinis* Brøgger, 1878 and *A. atavus*. The syntypes of *A. intermedius*, about 50 cephalon and pygidia preserved in partial relief, were collected from a black, organic-rich shale (alum shale) within the *P. atavus* Zone at the Verke rivulet in Andrarum, Scania (Fig. 1; locality 9 of Tullberg, 1880 and Moberg, 1910). *A. affinis*, *A. atavus*, and *A. intermedius* were subsequently assigned to *Ptychagnostus* (Jaekel, 1909; Kobayashi, 1939).

After reviewing syntypes and many other specimens, Westergård (1946) concluded that the differences between *P. atavus* and *Ptychagnostus intermedius* are not of specific value and may be due to preservation and individual variation. Thus, he synonymized the two taxa and first published photographs of specimens from each type series. Perhaps influenced by the fact that some of Westergård's photographs are significantly retouched, Öpik (1979) and Ergaliev (1980) independently reinstated *P. intermedius* as a valid species; Robison (1982, 1984, 1994) and Rowell et al. (1982) concurred. Ergaliev (1980: p. 69) also selected a syntype cephalon (Westergård, 1946: Pl. 11, Fig. 19; see Fig. 2(5)) as the lectotype of *P. intermedius* (for additional comment, see Robison, 1984: p. 25). Laurie (1988) further noted that the syntypes of *P. intermedius* are not well preserved and suggested that they may be conspecific with those of *P. affinis*, and he suggested that *Ptychagnostus sinicus* Lu, 1957 may be the valid name for specimens referred to *P. intermedius* by Robison and others.

Close examination of the type series of *P. intermedius* provides new information regarding taxonomy and affinities of the species. The cephalon (Fig. 2(5–7)) have moderately deep genal scrobiculae but lack paired crescentic scrobiculae near the anterior end of the glabella, and the median glabellar node is near the posteroglabellar midpoint. Although retouched, Westergård's (1946: Pl. 11, Fig. 19) illustration of the lectotype cephalon corresponds fairly well with the actual specimen (Fig. 2(5)) except for enlargement of the median glabellar node and restoration of the left lateral border. The other syntype cephalon illustrated by Westergård (1946: Pl. 11, Fig. 20) has not been located with certainty, and it may have been destroyed during an attempt to make a mould. Westergård's (1946: Pl. 11, Fig. 21) illustration of a syntype pygidium (LO3432t) differs significantly from our illustration (Fig. 2(8)). Most importantly, our illustration shows that the median tubercle is prominent and medially indents the F2, resulting in a distinctly hexagonal M2 similar to that in the syntype pygidium of *P. atavus* (Fig. 2(3)). In comparison, Westergård's retouched illustration incorrectly portrays a weaker tubercle and a straight F2. Of lesser import, the articulating half ring has been obliterated. Other syntype pygidia (Fig. 2(9–12)) also have a prominent tubercle that medially indents the F2 and the M2 is distinctly hexagonal. Although specimens in the type series of *P. intermedius* are less well preserved and more flattened than those in the type series of *P. atavus*, other differences in morphology are less than that seen within many populations of *P. atavus*, each from a single bed. Thus, we here agree with Westergård's (1946) suppression of *P. intermedius* as a subjective junior synonym of *P. atavus*.

As noted above, Laurie (1988: p. 178) suggested that the syntypes of *P. intermedius* and *P. affinis* may be conspecific. However, the median glabellar node on syntype cephalon of *P. intermedius* is near the M2 midpoint whereas it is far forward on the M2 of *P. affinis*. Syntype pygidia of *P. intermedius* have smooth pleural fields whereas those of *P. affinis* have a granular sculpture. Because they show no evidence of a transverse sulcus, the syntype pygidia of *P. intermedius* also likely differed by having a more convex posteroaxis. Therefore, we do not regard *P. affinis* and *P. intermedius* to be conspecific. The type

series of *P. intermedius* was collected at a lower stratigraphic level than that of *P. affinis*.

A review of the type series of *P. sinicus*, written for publication elsewhere, indicates that Laurentian agnostoids previously assigned to *P. intermedius* by Robison (1982, 1984, 1994) and Rowell et al. (1982) should be reassigned to *P. sinicus*. Comparative morphology and phylogenetic analysis, supported by stratigraphic occurrences, indicate that *P. sinicus* (as emended here) is the likely ancestor of *P. atavus* (Rowell et al., 1982). *P. sinicus* mainly differs from *P. atavus* by having a weaker median tubercle on the pygidial M2, which leaves the F2 either straight or with only a slight medial indentation. Therefore, the pygidial M2 of *P. sinicus* is usually pentagonal (rarely subrectangular) whereas it is distinctly hexagonal in *P. atavus*. *P. sinicus* is a common, widespread species in low palaeolatitudes with an observed stratigraphic range from the basal *P. gibbus* Zone to the lower *P. atavus* Zone. Subjective junior synonyms of *P. sinicus* include *Ptychagnostus idmon* Öpik, 1979 and *Ptychagnostus scarifatus* Öpik, 1979.

3. Concluding remarks

P. atavus is a distinctive ptychagnostid species. Its differential characters include a median node near or slightly posterior to the glabellar M2. A prominent, ovate, median tubercle distinctly indents the pygidial F2, resulting in a hexagonal M2. It also lacks spines and surface granulation. Some other characters varied either within populations or during ontogeny and we accord those no taxonomic significance. For example, genal scrobiculae may be absent or present, and if present, may vary markedly in depth (e.g. Robison, 1982). Also, crescentic, paired, genal scrobiculae near the anterior end of the glabella may be absent or present, and if present, may vary in depth. Ontogenetic series from Sweden and elsewhere show that the postaxial median furrow became weaker during growth and may be effaced in late holaspides (Westergård, 1946; Robison, 1982, 1984).

P. atavus is a common, easily identified species with global distribution in open-marine lithofacies, which makes its FAD an excellent marker for defining the base of a global Cambrian stage (e.g. Babcock et al., 2004, 2005). It has an observed stratigraphic range from the base of the *P. atavus* Zone to the lower *Ptychagnostus punctuosus* Zone.

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