THE ORDOVICIAN CONODONT GENUS *PYGODUS*

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Two evolutionary branches of *Pygodus* are recognized and discussed. The new species *Pygodus lunnensis* and *P. protoanserinus* are proposed and described in detail. It is suggested that *P. anserinus* did not evolve directly from *P. serra* but from *P. protoanserinus* sp. n. Two new subzones within the *Eoplacognathus suecicus* Zone are proposed: the *Pygodus lunnensis* and *P. anitae* Subzone.

Key words: Conodonta, *Pygodus*, Ordovician.

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Pygodus Lamont et Lindström, 1957 is one of the morphologically most distinct, and biostratigraphically most useful, of the Ordovician conodont genera. It was defined in terms of multielement taxonomy by Sweet and Bergström (1962), Bergström (1971) and Löfgren (1978). Species of Pygodus have pygodontiform, haddingodontiform and ramiform elements. Until now, three species have been assigned to Pygodus with certainty. These are: (1) Pygodus serra (Hadding, 1913), with three dентicle rows on the platform of the pygodontiform element; (2) Pygodus anserinus Lamont et Lindström, 1957, with four dентicle rows on the platform of the pygodontiform element; and (3) Pygodus anitae Bergström, 1983, with deep depression between the secondary antero-lateral and the anterior processes of the pygodontiform element.

The evolution of the Pygodus lineage, from P. serra to P. anserinus, was discussed by Bergström (1971, 1983) and Dzik (1976, 1983). P. serra and P. anserinus were used as conodont zonal indexes of the Middle Ordovician of eastern North America, Europe (Bergström 1971) and South China (An 1987). Bergström (1983) named Pygodus? sp. C of Löfgren (1978: p. 97; pl. 16: 4–6) Pygodus anitae and considered this species to be ancestral to P. serra.

When studying Ordovician conodonts from the Hälleks quarry, Västergötland, Central Sweden (Fig. 1), I found two kinds of pygodontiform elements with three dентicle rows on the platform. Despite obvious morphological differences, both the elements have hitherto been referred to Pygodus serra (Hadding). One of these elements is long and narrow. During its evolutionary history, its middle dентicle row migrated from the middle to the inner side (Fig. 2C1–C3). The other is triangular and its middle dентicle row migrated from the middle to the outer side (Fig. 2D).

According to the description and illustrations of Lamont and Lindström (1957: p. 68, fig. 1), Pygodus anserinus (the pygodontiform element) has “very small cusp, three rows of small, irregular dентicles, and in large specimens, a fourth row”. Its holotype has a weakly developed fourth dентicle row (fig. 1c). In fact, P. anserinus included a three row form in which the middle dентicle row is situated outside of the mid-line (Fig. 1d) and a primitive four row form of the species P. anserinus (Fig. 1a, b, c).

When Hamar (1964, 1966) studied the Middle Ordovician of the Oslo region, Norway, he found pygodontiform elements with three dентicle rows that diverge at small angles from the cusp and with the middle row running along the middle of the triangular platform. These elements occurred in the same sample together with Pygodus anserinus Lamont et Lindström (Hamar 1966: table 1). He assigned them to a new species Pygodus trimonitis. Bergström (1971) identified the three row forms as Pygodus serra (Hadding) and the four row forms to P. anserinus. He considered Arabellites serra Hadding, 1913 to be the haddingodontiform elements of P. serra and regarded

![Fig. 1](image-url)
Outline map of Sweden, showing the geographic location of the investigated sections.
The stratigraphic ranges and evolutionary relationships of five species of *Pygodus*. **A.** Pygodontiform element of *P. lunnensis* sp. n. (same specimen as Pl. 1: 13). **B1.** Early form of the pygodontiform element of *P. anitae* (same specimen as Pl. 1: 2). **B2.** Late form of the pygodontiform element of *P. anitae* (same specimen as Pl. 2: 15). **C1.** Early form of the pygodontiform element of *P. sera* (same specimen as Pl. 2: 11). **C2.** Middle form of the pygodontiform element of *P. sera* (same specimen as Pl. 2: 7). **C3.** Late form of the pygodontiform element of *P. sera* (same specimen as Pl. 2: 1). **D.** Pygodontiform element of *P. protoanserinus* sp. n. (same specimen as Pl. 3: 9). **E1.** Early form of the pygodontiform element of *P. anserinus* (same specimen as Pl. 3: 5). **E2.** Late form of the pygodontiform element of *P. anserinus* (same specimen as Pl. 3: 1).
**Conodont (Pygodus) zones and subzones of the Middle Ordovician in the Baltoscandic Region.**

P. trimonitis as probably an extreme variant of P. anserinus or as a survivor of the P. serra stock. Thus, P. trimonitis came to be dubiously listed in the synonymy of P. serra (Hadding). Since 1971, three row forms have been assigned to P. serra. Recently, three row and four row forms were found in the same samples (D156 and D160) in southern Uplands of Scotland by Armstrong (1997), who considered the three row form to be a Pb element of P. anserinus and the four row form to be a Pa element of P. anserinus.

My collection include many specimens of Pygodus from Sweden (Fig. 1) as well as three sections from China: (1) Tangshan section, Nanjing City, Jiangsu Province (Chen and Zhang 1984); (2) Dinxia section, Shitai County, Anhui Province (Chen and Zhang 1989); and (3) Fenxiang section, Yichang County, Hubei Province (Zhang 1996). I present here a detailed study devoted to the pygodontiform element of the genus Pygodus from upper Abereiddian to Llandeilian (cf. Fortey et al. 1995; see Fig. 3), a stratigraphic range that corresponds to Aserian to Uhakanian (Jaanusson 1995). The research shows that, the upper Abereiddian (Aserian) to the Llandeilian, the pygodontiform element underwent morphological evolution that was primarily characterized by the diminution of the posterior process, and the merging together of the platform ledges of the postero-lateral process and the anterior process. One of the three row forms, described here as Pygodus protoanserinus sp. n., is morphologically intermediate between P. serra and P. anserinus. Thus, P. protoanserinus sp. n. (not P. serra) is considered here as a direct ancestor of P. anserinus. Consequently, two evolutionary branches can be distinguished in the late stage of the Pygodus lineage history (Fig. 2). Pygodus? sp. B of Lofgren (1978: p. 97; pl. 16: 2, 3) is named here as the new species Pygodus lunnensis, which is probably the oldest species of this genus.

The conodont elements illustrated in the Figures and Plates are deposited in the Department of Geology and Geochemistry, University of Stockholm, Sweden.

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THE EVOLUTION OF THE PYGODUS LINEAGE

The evolution of Pygodus is mainly manifested by the morphological changes of the pygodontiform element.

The pygodontiform element of Pygodus lunnensis sp. n., the oldest known species of the genus, has four processes: anterior, antero-lateral, posterior and postero-lateral. The secondary antero-lateral process developed between the anterior and the antero-lateral processes (Fig. 4A, Pl. 1: 12, 13). Sometimes there are two denticle rows on the anterior process (LÖFGREN 1978: pl. 16: 2).

A possible descendant of P. lunnensis sp. n. is Pygodus anitae BERGSTROM, 1983. The evolutionary changes involved reduction of the posterior process: it became a short posterior extension of the platform below the cusp (Pl. 1: 1, 8, 9). The anterior process remained wide with two denticle rows (Fig. 2B1, B2; Pl. 1: 1, 2, 5, 6, 8; Pl. 2: 15, 16). The angle of the postero-lateral with the antero-lateral processes decreased. The platform ledge of the postero-lateral process merged with the anterior process. Sometimes, the postero-lateral process disappeared (Pl. 1: 1, 5, 6; Pl. 2: 16). In the stratigraphically younger specimens the secondary antero-lateral process became short and close to the antero-lateral process (Fig. 2B2; Pl. 2: 15, 16) and a deep depression between the secondary antero-lateral process and the anterior process (Fig. 2B1, B2; Pl. 1: 1, 2, 5, 6) developed.

Because of the merging of the processes and the disappearance of the secondary antero-lateral and postero-lateral processes, it is appropriate, for the younger species, to refer to the outer denticle row on the anterior process as the middle denticle row, to the inner denticle row on the anterior process as the inner denticle row, and to the denticle row of the antero-lateral process as the outer denticle row (Fig. 4).

Fig. 4
Orientation of pygodontiform elements. A. Pygodus lunnensis sp. n., same specimen as Pl. 1: 13. B. Pygodus serra, same specimen as Pl. 2: 11. C–G show the change of the denticle rows on the processes from P. lunnensis sp. n. (C) to P. anitae (D), P. serra (E), P. protoanserinus sp. n. (F), and to P. anserinus (G).
The depression between the middle and outer denticle rows gradually became shallow. This evolutionary phase is represented by Pygodus serra (HADDING). P. serra (HADDING) sensu LÖFGREN (1978: p. 98, fig. 32D–F), from the E. foliaceus Subzone, represents an older variant of this species, the inner ledge of the pygodontiform element being wide.

There are two evolutionary branches recorded in the younger strata. One branch, without noticeable changes, is here still referred to as P. serra. In this lineage, three denticle rows are smoothly concave to the inside, and the platforms are narrow and long. (Fig. 2C1–C3; Pl. 2: 1, 2, 6, 7, 11, 12, 14). The distance between the middle and inner denticle rows is slightly shorter than the distance between the middle and outer denticle rows.

Another evolutionary branch is a lineage from Pygodus protoanserinus sp. n. to Pygodus anserinus LAMONT et LINDSTRÖM. There are also three denticle rows on the platform of pygodontiform elements of P. protoanserinus sp. n. However, the distance between the middle and inner denticle rows is greater than between the middle and outer ones. The denticles in the inner denticle row are thicker than in the other rows (Fig. 2D; Pl. 3: 9, 10, 14). The ridges between denticle rows are straight on the inside of the platform. This species was previously identified as P. anserinus, P. serra and P. sp. cf. P. serra (see synonymy).

The new denticle row appears between the middle and inner denticle rows. The number of denticles in this new denticle row gradually increases in the younger strata. In the specimens from the youngest strata, the new denticle row starts near the cusp (Fig. 2E1, E2; Pl. 3: 1, 2, 5, 6). The ridges beside the new row are curved. This evolutionary phase of the four row form is represented by Pygodus anserinus. It is the youngest known species of the Pygodus lineage. It became extinct in the early Caradoc (BERGSTROM 1983).

The most obvious change of the haddingodontiform elements is that the angle between the posterior process and the anterior process gradually increased from about 50° in P. lunensis sp. n. (Pl. 1: 14) to more than 100° in P. anserinus (Pl. 3: 3). The morphological evolution of the ramiform elements is not so obvious. The observable change is that the base gradually became narrow and small. For these reasons, it is difficult to identify the species based on the haddingodontiform and ramiform elements.

## STRATIGRAPHIC DISTRIBUTION AND SIGNIFICANCE

*Pygodus* occurs from the Eoplacognathus suecicus Zone to Amorphognathus tvaerensis Zone (the upper part of Abereridian to Llandeilo, Fig. 3). The *E. suecicus* Zone, as referred to in this paper, corresponds to the BERGSTROM’s *E. suecicus* Subzone and the major part of LÖFGREN’S *E. suecicus* – Panderodus sulcatus assemblage subzone, which will be discussed further in another paper.

The oldest species of the *Pygodus* lineage, *P. lunensis* sp. n., appears to be restricted to the lower part of the Segerstad Limestone of Sweden. The limestone corresponds to the lower part of the *E. suecicus* Zone (Fig. 5A). It is known from the sections Lunné, Kullstaberg and Gusta (LÖFGREN 1978), Province of Jämtland in Sweden.

The second oldest species, *P. anitae*, ranges from the upper part of the Segerstad Limestone to the base of the Seby Limestone in Sweden, i.e., the units that correspond to the upper part of the *E. suecicus* Zone and the lower part of the *E. foliaceus* Subzone. *P. anitae* was found in the Lunné (Fig. 5A), Kullstaberg, and Gusta sections (LÖFGREN 1978) in Jämtland, at Kågårde and Vikarbyn, Siljan district of Sweden (BERGSTROM 1983) and in the Ordos Basin, North China (AN and ZHENG 1990). *P. lunensis* sp. n. and *P. anitae* have not been found in South China.

*Pygodus serra* (HADDING) ranges from the lower part of the *E. foliaceus* Subzone to the lower part of *Pygodus anserinus* Zone (Fig. 2). It occurs in the Baltoscandic area (HAMAR 1966; BERGSTROM 1971; LÖFGREN 1978; DZIK 1994), China (AN 1987: pl. 26: 1, 2, 4, 5; AN and ZHENG 1990: pl. 13: 20, 21; CHEN and ZHANG 1984: pl. 1: 12, 13) and Scotland (ARMSTRONG 1997: pl. 4: 4). *Pygodus serra* (HADDING) was distinguished as the index species of the zone by BERGSTROM (1971).

*Pygodus protoanserinus* sp. n. occurs from the *E. robustus* Subzone to the *E. Lindstroomi* Subzone (Fig. 2). It is very widely distributed including; the Baltoscandic area (LAMONT and LINDSTRÖM 1957; HAMAR 1966; BERGSTROM 1971, 1983; DZIK 1976, 1983, 1994), Scotland (BERGSTROM and ORCHARD 1985, BERGSTROM 1990), North America (LINDSTRÖM 1964; BERGSTROM 1971; BERGSTROM and CARNES
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*Pygodus anserinus* is similar in its geographic distribution to *P. protoanserinus* sp. n. *P. anserinus* was established as the index species of the *P. anserinus* Zone by Bergstrom (1971).
Pygodus serra and P. anserinus are index fossils of conodont zones in the Baltoscandic area, eastern North America and central China. The P. serra Zone was subdivided into five subzones by BERGSTROM (1971). He used Eoplacognathus suecicus, which was found in the Aserian, as an index for the lowermost subzone of the P. serra Zone (Figs 3, 5A). LÖFGREN (1978) found that P. serra first appeared at the slightly higher level of E. foliaceus, which occurs in the Lasnamaegian. She proposed that the base of the P. serra Zone should be correlated with the base of the E. foliaceus Subzone. The present investigation supports LÖFGREN's suggestion, namely, that the P. serra Zone includes four subzones (Fig. 3).

In summary, P. anitae is restricted to the upper part of the Segerstad Limestone and the basal part of the Seby Limestone. P. lunnensis sp. n. occurs in the lower part of the Segerstad Limestone. Both can be used as index fossils. The P. anitae and P. lunnensis Subzones are hereby established as subzones of the E. suecicus Zone (Figs 3, 5A).

**Pygodus lunnensis Subzone**

**Definition.** — The lower boundary of the subzone coincides with the first appearance of E. suecicus and P. lunnensis sp. n. The upper boundary is taken to be just below the first appearance of P. anitae.

**Reference section.** — Lunne section (Fig. 5A). The base of this subzone is situated at 8.2 m, and the top is situated at 5.35 m. This subzone is 2.85 m thick in this section.

**Pygodus anitae Subzone**

**Definition.** — The lower boundary of the subzone coincides with the first appearance of P. anitae. The upper boundary is defined as the level at which E. foliaceus first appears.

**Reference section.** — Lunne section (Fig. 5A). The base of this subzone is situated at 5.35 m, and the top is situated at 3.12 m. This subzone is 2.23 m thick in this section.

The overlap of the ranges of P. serra and P. anserinus was reported by FÄHRÉUS and HUNTER (1981), FÄHRÉUS (1982) and AN et al. (1985). In fact, P. serra (HADDING) sensu AN et al. (1985) belongs to P. protoanserinus sp. n. There are no figures of P. serra in FÄHRÉUS and HUNTER (1981) and FÄHRÉUS (1982). According to three pygodontiform elements from the sample CTH14 of Cottles Island section, New World Island, north-central Newfoundland, P. serrus (HADDING) sensu FÄHRÉUS et HUNTER is also P. protoanserinus sp. n. The number of denticles in the fourth denticle row of the pygodontiform element gradually increases from the anterior ledge to the cusp. This implies gradual evolution from P. protoanserinus sp. n. to P. anserinus. If the part with denticles of the fourth denticle row were broken off, it would be difficult to separate the early form of P. anserinus from the later form of P. protoanserinus sp. n. It seems that the ranges of P. protoanserinus sp. n. and P. anserinus overlap (e.g. my samples HÅL17.05 and HÅL18.48, see Fig. 5B).

P. protoanserinus sp. n. and P. anserinus occur repeatedly three times at Quarry Cove section, New World Island, north-central Newfoundland (FÄHRÉUS and HUNTER 1981: fig 2, table 1; FÄHRÉUS 1982: fig. 2). FÄHRÉUS (1982: p. 6) concluded that speciation of P. anserinus was allopatric, leaving a surviving parent species. However, it is possible that the repetition was caused by faulting, assuming that the identification of species is correct.

**PHYLOGENETIC RELATIONSHIPS OF PYGODUS**

LÖFGREN (1978) stressed that in the platform elements of Pygodus and Polonodus DZIK, 1976 the anterior platforms are much better developed than the posterior one. This was taken as an indication of a closer relationship between Pygodus and Polonodus than between either of them and the contemporary Eoplacognathus, in which similar elements have a much larger posterior than anterior platform. BERGSTROM (1983) derived Pygodus from Polonodus based on specimens from the early Llanvirn. DZIK (1983) suggested that Pygodus evolved from early prioniodontids, the elements of which were described as Fryxellodontus? ruedemannii by LANDING (1976) from the early Arenig Oepikodus evae Zone.
LOFGREN (1990) described in detail the platform elements of Polonodus and believed them to be associated with oistodontiform and ramiform elements. The apparatus of Pygodus does not contain oistodontiform elements. The pygodontiform elements of Pygodus lunnensis sp. n. (Fig. 2A) have the same branching type as the corresponding elements of Polonodus. The haddingodontiform elements of Pygodus lunnensis sp. n. have three processes (Pl. 1: 14) and are very similar to corresponding elements of the later Pygodus species, but the corresponding elements of Polonodus have four processes. Generic assignment of Pygodus lunnensis sp. n. is based on the form of the haddingodontiform element and the absence of the oistodontiform element.

The suggested close evolutionary relationship between Pygodus and Polonodus is supported by the same distinctive branching type of pygodontiform elements of Pygodus lunnensis sp. n. and the corresponding elements of Polonodus. The early morphological evolution of the pygodontiform element of the genus Pygodus consisted mainly of the reduction of the posterior process, and the merging of the platform ledges of the postero-lateral process and the anterior process.

**SYSTEMATIC PALEONTOLOGY**

Genus *Pygodus* LAMONT et LINDSTROM, 1957

Type species: *Pygodus anserinus* LAMONT et LINDSTROM, 1957.

*Pygodus lunnensis* sp. n.

(Pl. 1: 12–16; Figs 2A, 4A)


Holotype: The specimen SO-9501 figured on Pl. 1: 13, Fig. 2A, and Fig. 4A.

Type horizon: Sample Lu6.00 of the Segerstad Limestone (Fig. 5A).

Type locality: Lunne, about 2.6 km E of Brunflo, 300 m south of the road between Brunflo and Rissna, Jämtland, Sweden (Fig. 1; LARSSON 1973: fig. 2).

Derivation of name: Referring to Lunne village, Jämtland, Sweden.

**Diagnosis.** — The angle between the postero-lateral and antero-lateral processes of the pygodontiform element is 100–120 degrees and the platform ledge of the antero-lateral process merges with the anterior process. The haddingodontiform element has three weakly denticulated processes.

**Material.** — Pygodontiform elements (n = 21), haddingodontiform elements (n = 14), ramiform elements (n = 52).

**Description.** — Pygodontiform (stelliscaphate) elements have four processes: anterior, antero-lateral, posterior, and postero-lateral (Fig. 4A; Pl. 1: 12, 13). The posterior process is short, wide, and round. The postero-lateral process is close to the anterior one. The antero-lateral process is wider and longer than other processes and is overgrown by a secondary antero-lateral process. The platform ledges of the anterior and antero-lateral processes are confluent. The concavity between the postero-lateral and anterior processes is deeper than that between the antero-lateral and anterior processes. The surface of the platform is ornamented with contoured ridges.

The haddingodontiform (pastinate) element has a suberect cusp, and weakly denticulated antero-lateral, anterior, and posterior processes. The angle between the anterior and posterior processes is about 50 degrees (Pl. 1: 14).

This species has three kinds of ramiform elements. They are the alate, tertiopedate (Pl. 1: 16), and quadriramate (Pl. 1: 15) elements with suberect cusps and wide, deep bases.

**Occurrence.** — Lower part of the Segerstad Limestone, *P. lunnensis* Subzone, corresponding to the lower part of the *E. suecicus* Zone. The description is based on specimens from the Lunne and Kullstaberg sections, Jämtland, Sweden (Fig. 5A).
Pygodus serra (Hadding, 1913)
(Pl. 2: 1–14; Figs 2C1–C3, 4B)

1966. Pygodus trimontis n. sp.; Hamar: p. 70, pl. 7: 12, 16, 17.
1967. Haddingodous serra (Hadding); Viira: fig. 4: 7.
1971. Pygodus serra (Hadding); Bergström: p. 149, pl. 2: 22, 23.
1974. Pygodus serrus (Hadding); Bergström et al.: pl. 1: 18.
1978. Pygodus serra (Hadding); Lofgren: p. 98, fig. 32D–F.
1984. Pygodus serrus (Hadding); Chen and Zhang: p. 329, pl. 2: 12, 13, 21, 22 (non 9–11, 18–20).
1987. Pygodus serrus (Hadding); Hünicken and Ortega: p. 140, pl. 7: 1: 3.
1987. Pygodus serrus (Hadding); An: pl. 26: 1, 2, 4, 5 (non 3, 6–8).
1994. Pygodus serra (Hadding); Dzik: p. 103, pl. 17: 9–12, fig. 26 (non the pygodontiform element to the left in the fifth row counted from below).

Material. — Pygodontiform elements (n = 137), haddingodontiform elements (n = 88), and ramiform elements (n = 34).

Discussion. — P. serra differs from P. protoanserinus sp. n. in the following aspects: (1) the pygodontiform elements of P. serra the three denticle rows are smoothly concave to the inside; (2) the platform in P. serra is narrow and long; (3) and the middle denticle row of P. serra is in the middle or in the interior part. The shape of the pygodontiform elements of P. serra varies across stratigraphic levels. In the lower part of the E. foliaceus Subzone, the inside ledge is wide (Lofgren 1978: fig. 32D). In the E. reclinatus Subzone, the ridges are strongly concave to ward the aboral side (Fig. 2C1). From the E. robustus Subzone to the E. lindstroemi Subzone, the platform is narrow and long (Fig. 2C2, 2C3).


Arabellites serra Hadding, 1913 is the haddingodontiform element of Pygodus. Because the haddingodontiform elements of P. serra are similar to those of P. protoanserinus sp. n., it is uncertain if A. serra Hadding (1913: pl. 1: 12, 13) does indeed represent the haddingodontiform elements of P. serra Hadding sensu Bergström 1971. This could probably be ascertained by checking the topotype material including pygodontiform elements collected by Hadding (1913) and Bergström (1971: p. 150).

Occurrence. — From the lower part of the E. foliaceus Subzone to the lower part of the P. anserinus Zone (Fig. 2). The specimens described here were obtained from the Skövde and Gullhögen Limestones of the Hälleki section, Sweden (Fig. 5B).

Pygodus protoanserinus sp. n.
(Pl. 3: 9–18; Fig. 2D)

1957. Pygodus anserinus n. sp.; Lamont et Lindström: p. 68 (pars), fig. 1d (non a–c).
1976. Pygodus serra (Hadding); Dzik: fig. 29a, b.
1979. Pygodus serra (Hadding); Harris et al.: pl. 2: 18.
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1982. *Pygodus serrus* (HADDING); AN and DING: pl. 5: 13, 14, 16, 19, 22.
1987. *Pygodus serrus* (HADDING); BERGSTROM and ORCHARD: pl. 2.2: 5
1987. *Pygodus serrus* (HADDING); AN: p. 177, pl. 26: 3, 6, 13, (non 1, 2, 4, 5), pl. 29: 2, 3.
1989. *Pygodus serrus* (HADDING); CHEN and ZHANG: pl. 5: 1, 2.
1994. *Pygodus serrus* (HADDING); Dzik: fig. 26: only one pygodontiform element first to the left, fifth row from below.

Holotype: The specimen SO-9557 figured on Pl. 3: 9, and Fig. 2D.
Type horizon: Sample Hål 16.64, the middle of Gullhögen Limestone (Fig. 5B).
Type locality: Hälleksis, Västergötland, Sweden (Fig. 1).
Derivation of name: From Latin proto, primitive, and anser, goose, referring to the evolutionary relationship of the species with *Pygodus anserinus*, which has four denticle rows on the platform.

**Diagnosis.** — Pygodontiform element with the middle denticle rows situated to the outside of the middle.

**Material.** — Pygodontiform elements (n = 89), haddingodontiform elements (n = 95), and ramiform elements (n = 76).

**Description.** — The pygodontiform elements resemble the feet of geese and have three denticle rows on the platform. The distance between the middle and inner denticle rows is greater than between the middle and outer denticle rows. The denticles in the inner denticle row are thicker than in the other rows. The ridges are straight or arcuate on the inside of the platform (Pl. 3: 9, 10, 14). Sometimes, there are one or more nodes on the ridge on the inside of the platform (Pl. 3: 9).

The haddingodontiform (Pl. 3: 11, 16) and ramiform (Pl. 3: 12, 13, 15, 17, 18) elements are similar to corresponding elements in *Pygodus serrra*.

**Comments on the synonymy list.** — The elements figured by Wolska (1961: pl. 5: 5), and Dzik (1976: fig. 29a, b) are from the *E. robustus* Subzone. Specimens occurring together with *E. protoramosus* CHEN et al., 1983, corresponding to the *E. lindstroemi* Subzone, were figured by CHEN and ZHANG (1984: pl. 2: 9–11). The pygodontiform element figured by Dzik (1994: fig. 26: only the first pygodontiform element from the left of the fifth row from below) was found in the *E. lindstroemi* Subzone.

McCRACKEN (1991) also observed that there are nodes on the inside of the platform of the pygodontiform element. The pygodontiform elements of *P. cf. P. serrra* (HADDING) figured by Nowlan (1981: pl. 2: 16–19) are probably primitive forms of *P. anserinus*.

**Occurrence.** — *E. robustus* and *E. lindstroemi* subzones (Fig. 2D). The specimens described here were obtained from the Gullhögen Limestone of the Hälleksis section, Västergötland, Sweden (Fig. 5B).

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Pygodus anitae BERGSTRÖM

1–4 from Kullstaberg section, Jämtland, Sweden, 5–11 from Lunne quarry, Jämtland, Sweden.

1. Pygodontiform element, × 40, upper view, sample 95FF01, SO-9631.
2. Pygodontiform element, × 40, upper view, sample 94FF30, SO-9625.
3. Tertiopedate element, × 40, lateral view, sample 94FF03, SO-9629.
4. Haddingodontiform element, × 40, lateral view, sample 94FF02, SO-9630.
5. Pygodontiform element, × 35, upper view, sample Lu5.10, SO-9518.
6. Pygodontiform element, × 55, upper view, sample Lu3.65, SO-9510.
9. Same specimen as 16a, × 120.
10. Quadriramate element, × 60, postero-lateral view, sample Lu4.50, SO-9515.
11. Alate element, × 70, posterior view, sample Lu3.65, SO-9514.

Pygodus lunnensis sp. n.

From Lunne quarry, Jämtland, Sweden.

12. Pygodontiform element, × 58, upper view, sample Lu5.50, SO-9502.
13. Pygodontiform element, holotype, × 30, upper view, sample Lu6.00, SO-9501.
14. Haddingodontiform element, × 55, lateral view, sample Lu7.00, SO-9504.
15. Quadriramate element, × 70, lateral view, sample Lu7.00, SO-9506.
16. Tertiopedate element, × 70, postero-lateral view, sample Lu7.00, SO-9507.
THE ORDOVICIAN CONODONT GENUS *Pygodus*

PLATE 2

*Pygodus serra* (HADDING) ............. 96

From Hälleks quarry, Västergötland, Sweden.

1. Pygodontiform element, $\times$ 60, upper view, sample HÅL15.95, SO-9537.
2. Pygodontiform element, $\times$ 55, upper view, sample HÅL15.95, SO-9536.
3. Haddingodontiform element, $\times$ 60, lateral view, sample HÅL15.95, SO-9538.
4. Tertiopedate element, $\times$ 70, postero-lateral view, sample HÅL15.95, SO-9540.
5. Alate element, $\times$ 80, posterior view, sample HÅL15.95, SO-9541.
6. Pygodontiform element, $\times$ 70, upper view, sample HÅL12.18, SO-9543.
7. Pygodontiform element, $\times$ 90, upper view, sample HÅL12.18, SO-9542.
8. Haddingodontiform element, $\times$ 80, lateral view, sample HÅL12.18, SO-9544.
9. Quadriramate element, $\times$ 90, lateral view, sample HÅL12.18, SO-9545.
10. Alate element, $\times$ 80, posterior view, sample HÅL12.18, SO-9546.
11. Pygodontiform element, $\times$ 80, upper view, sample HÅL11.69, SO-9548.
12. Pygodontiform element, $\times$ 80, upper view, sample HÅL11.69, SO-9549.
13. Haddingodontiform element, $\times$ 90, lateral view, sample HÅL11.69, SO-9554.
14. Pygodontiform element, $\times$ 80, upper view, sample HÅL11.69, SO-9547.

*Pygodus anitae* BERGSTROM (late form) ............. 91

From *E. foliaceus* Subzone at Lunne quarry, Jämtland, Sweden.

15. Pygodontiform element, $\times$ 68, upper view, sample Lu2.72, SO-9632.
16. Pygodontiform element, $\times$ 68, upper view, sample Lu2.72, SO-9633.
17. Haddingodontiform element, $\times$ 68, lateral view, sample Lu2.72, SO-9634.
18. Haddingodontiform element, $\times$ 68, posterior view, sample Lu2.72, SO-9635.
19. Tertiopedate element, $\times$ 68, postero-lateral view, sample Lu2.72, SO-936.
20. Alate element, $\times$ 68, posterior view, sample Lu2.72, SO-9637.
THE ORDOVICIAN CONODONT GENUS *PYGODUS*

PLATE 3

*Pygodus anserinus* (LAMONT et LINDSTRÖM) ................................. 92

From Hällekis quarry, Västergötland, Sweden.

2. Pygodontiform element, × 55, upper view, sample HÄL19.00, SO-9522.
4. Tertiopedate element, × 70, posterior view, sample HÄL19.00, SO-9524.
5. Pygodontiform element, × 55, upper view, sample HÄL17.05, SO-9556.
6. Same specimen as 5, × 160.
7. Quadriramate element, × 60, lateral view, sample HÄL21.11, SO-9521
8. Alate element, × 75, posterior view, sample HÄL19.00, SO-9525.

*Pygodus protoanserinus* sp. n .................................................. 96

From Hällekis quarry, Västergötland, Sweden.

10. Pygodontiform element, × 80, upper view, sample HÄL16.64, SO-9558.
11. Haddingodontiform element, × 70, lateral view, sample HÄL16.64, SO-9528.
12. Tertiopedate element, × 80, posterior view, sample HÄL16.64, SO-9530.
13. Quadriramate element, × 80, lateral view, sample HÄL16.64, SO-9529.
15. Quadriramate element, × 60, lateral view, sample HÄL12.90, SO-9533.
17. Tertiopedate element, × 80, posterior view, sample HÄL12.90, SO-9534.
18. Alate element, × 80, posterior view, sample HÄL12.90, SO-9535.