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 *Eoplacognthus suecicus* Zone are proposed: the *Pygodus lunnensis* and *P. anitae* Subzone.

Key words: Conodonta, *Pygodus*, Ordovician.

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INTRODUCTION

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 denticle rows on the platform of the pygodontiform element; (2) *Pygodus anserinus* LAMONT *et* LINDSTRÖM, 1957, with four denticle 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.

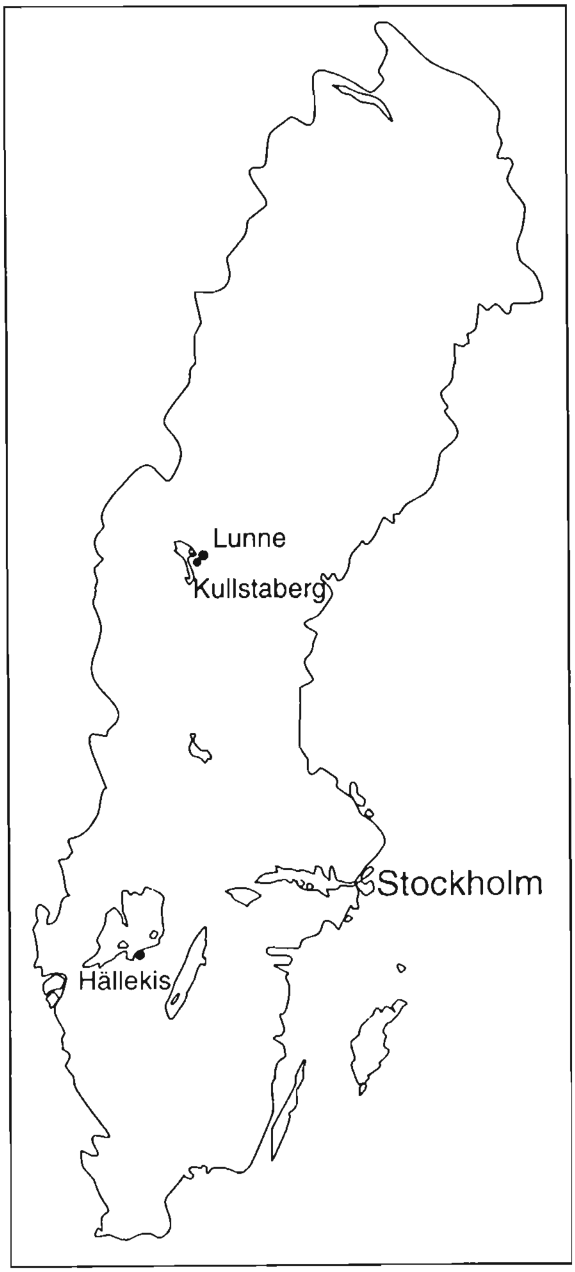

Fig. 1
Outline map of Sweden, showing the geographic location of the investigated sections.

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 Hällekis quarry, Västergötland, Central Sweden (Fig. 1), I found two kinds of pygodontiform elements with three denticle 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 denticle row migrated from the middle to the inner side (Fig. 2C1–C3). The other is triangular and its middle denticle 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 denticles, and in large specimens, a fourth row". Its holotype has a weakly developed fourth denticle row (fig. 1c). In fact, *P. anserinus* included a three row form in which the middle denticle 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 denticle 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 trimontis*. 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

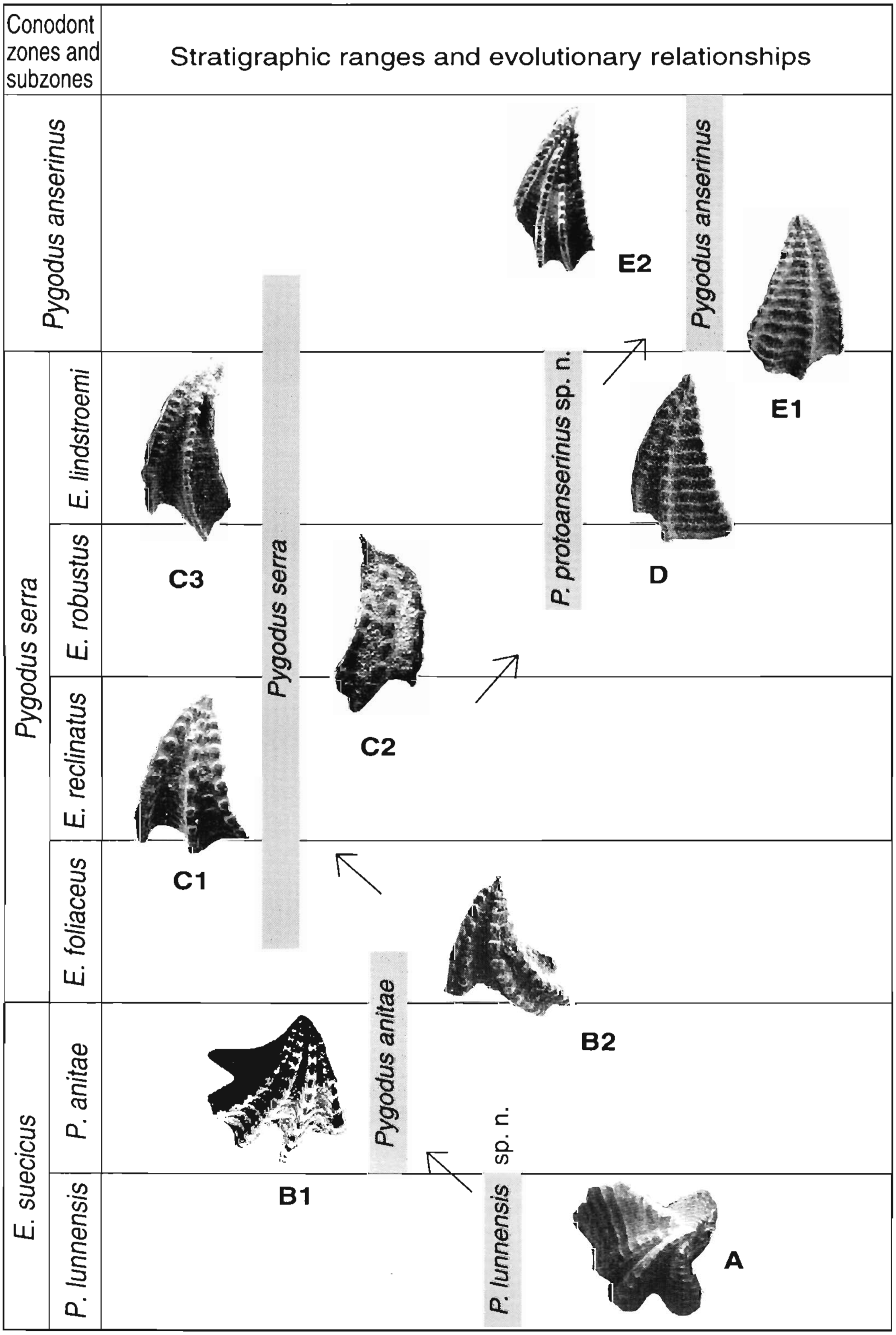

Fig. 2

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. serra* (same specimen as Pl. 2: 11). **C2**. Middle form of the pygodontiform element of *P. serra* (same specimen as Pl. 2: 7). **C3**. Late form of the pygodontiform element of *P. serra* (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).

<table>
<tr><td colspan="2">British stages and substages</td><td>Baltic stages</td><td colspan="6">Conodont zones and subzones</td></tr>
<tr><td colspan="2">Fortey et al. 1995</td><td>Jaanusson 1982, 1995</td><td colspan="2">Bergström 1971</td><td colspan="2">Löfgren 1978</td><td colspan="2">This paper</td></tr>
<tr><td rowspan="8">Llanvirn</td><td rowspan="4">Llandeilian</td><td rowspan="2">Kukruse</td><td colspan="2">Amorphognathus tvaerensis</td><td colspan="2" rowspan="5"></td><td colspan="2"></td></tr>
<tr><td colspan="2">Pygodus anserinus</td><td colspan="2">Pygodus anserinus</td></tr>
<tr><td rowspan="2">Uhaku</td><td rowspan="4">Pygodus serra</td><td>E. lindsrtroemi</td><td rowspan="4">Pygodus serra</td><td>E. lindstroemi</td></tr>
<tr><td>E. robustus</td><td>E. robustus</td></tr>
<tr><td rowspan="4">Abereiddian</td><td rowspan="2">Lasnamaegi</td><td>E. reclinatus</td><td>E. reclinatus</td></tr>
<tr><td>E. foliaceus</td><td>P. serra</td><td>E. foliaceus</td><td>E. foliaceus</td></tr>
<tr><td rowspan="2">Aseri</td><td colspan="2" rowspan="2">Eoplacognathus suecicus</td><td rowspan="2">E. suecicus</td><td rowspan="2">E. suecicus-P. sulcatus</td><td rowspan="2">E. suecicus</td><td>Pygodus anitae</td></tr>
<tr><td>Pygodus lunnensis</td></tr>
</table>

Fig. 3
Conodont (*Pygodus*) zones and subzones of the Middle Ordovician in the Baltoscandic Region.

P. trimontis as probably an extreme variant of *P. anserinus* or as a survivor of the *P. serra* stock. Thus, *P. trimontis* 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 ARMSTORNG (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) Dinxiang 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 Uhakuan (JAANUSSON 1995). The research shows that, the upper Abereiddian (Aserian) to the Llandeilian, the pygodontiform element underwent morphological evolution that was primrily 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 LÖFGREN (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* BERGSTRÖM, 1983. The evolutionary changes involved reduction of the posterior process: it became a short posterior extension of the platform below the cusp (Pl. 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 posterio-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).

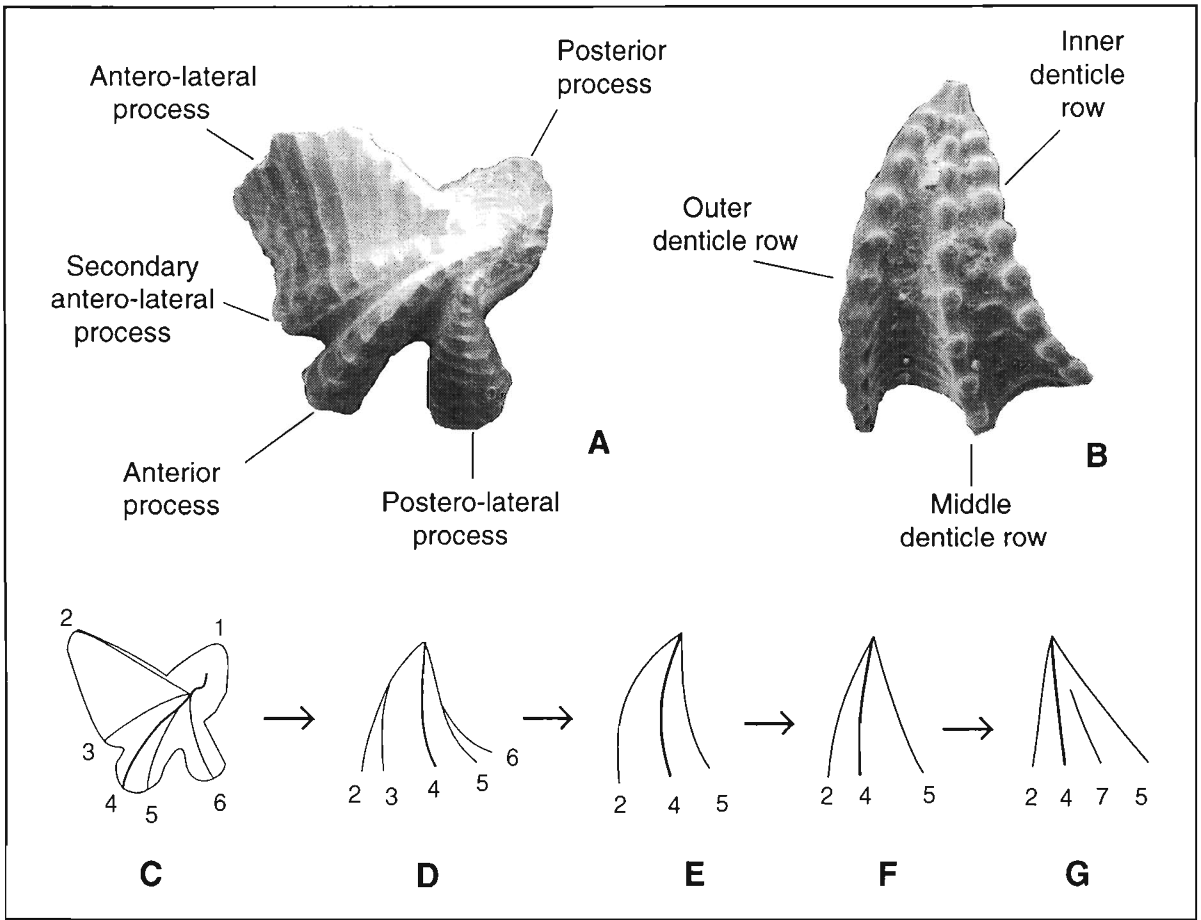

Fig. 4
Orientation of pygodontiform elements. **A**. *Pygodus lunnensis* sp. n., same specimen as Pl. 1: 13. **B**. *Pygodus serra*, same specimen as Pl. 2: 11. **C–G** show the change of the denticle rows on the processes from *P. lunnensis* sp. n. (**C**) to *P. anitae* (**D**), *P. serra* (**E**), *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 identifies 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 (BERGSTRÖM 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. lunnensis* 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 Abereiddian to Llandeilo, Fig. 3). The *E. suecicus* Zone, as referred to in this paper, corresponds to the BERGSTRÖM'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. lunnensis* 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 Lunne, 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 Lunne (Fig. 5A), Kullstaberg, and Gusta sections (LÖFGREN 1978) in Jämtland, at Kårgärde and Vikarbyn, Siljan district of Sweden (BERGSTRÖM 1983) and in the Ordos Basin, North China (AN and ZHENG 1990). *P. lunnensis* 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; BERGSTRÖM 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 BERGSTRÖM (1971).

Pygodus protoanserinus sp. n. occurs from the *E. robustus* Subzone to the *E. lindstroemi* Subzone (Fig. 2). It is very widely distributed including: the Baltoscandic area (LAMONT and LINDSTRÖM 1957; HAMAR 1966; BERGSTRÖM 1971, 1983; DZIK 1976, 1983, 1994), Scotland (BERGSTRÖM and ORCHARD 1985, BERGSTRÖM 1990), North America (LINDSTRÖM 1964; BERGSTRÖM 1971; BERGSTRÖM and CARNES

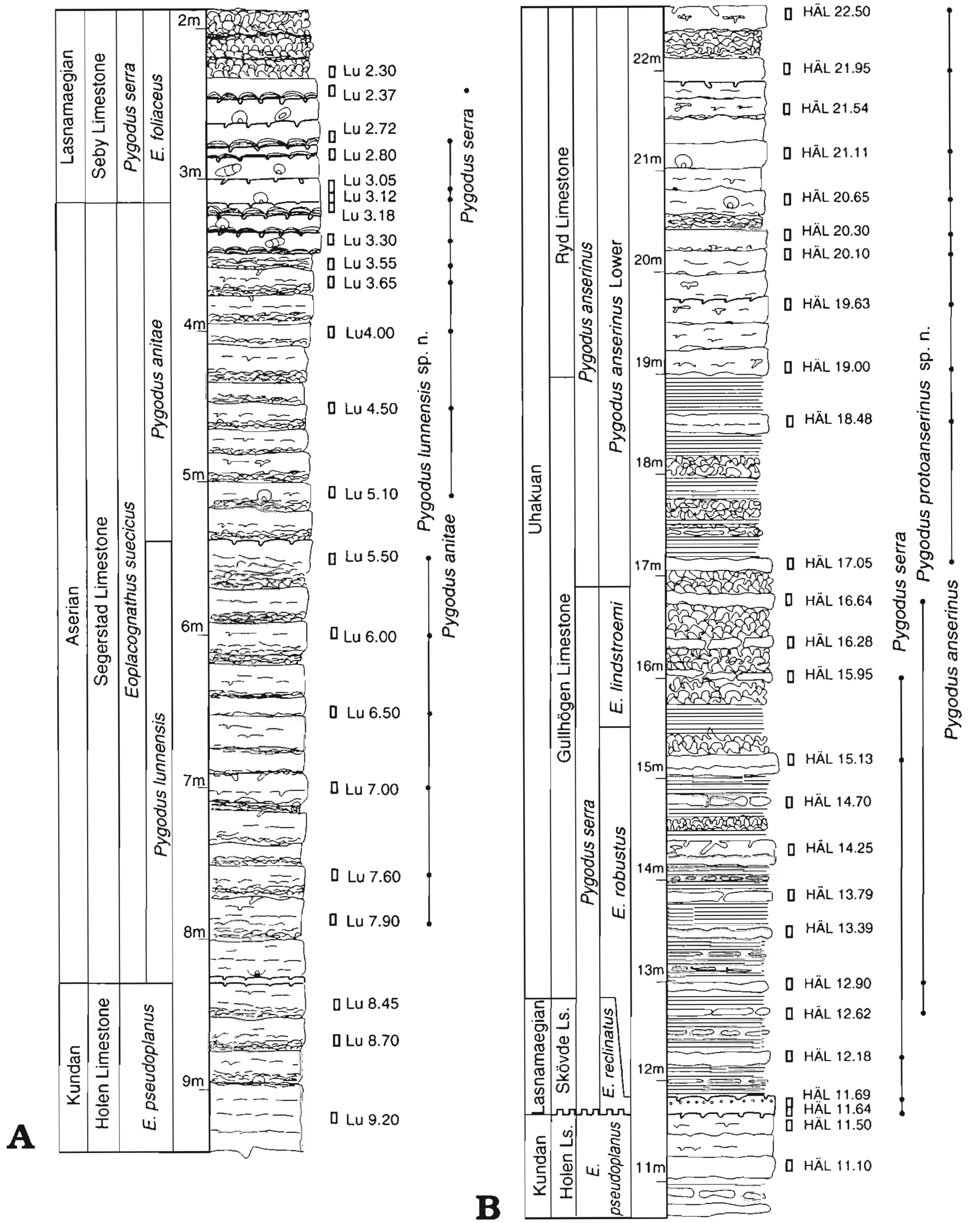

Fig. 5

A. The Lunne section (left), lithology, sampled levels, and ranges of *Pygodus lunnensis* sp. n., *P. anitae* and *P. serra*. **B**. The Hällekis section (right), lithology, sampled levels, and ranges of *Pygodus serra*, *P. protoanserinus* sp. n., and *P. anserinus*.

1976; FÅHRÆUS and HUNTER 1981; HARRIS *et al.* 1979; MCCRACKEN 1991), and China (AN 1981, 1987; AN and ZHENG 1990; CHEN and ZHANG 1984, 1989).

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 BERGSTRÖM (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 BERGSTRÖM (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 corelated with the base of the *E. foliaceus* Subzone. The present investigation supports LÖFGRENS 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 FÅHRÆUS and HUNTER (1981), FÅHRÆUS (1982) and AN *et al.* (1985). In fact, *P. serrus* (HADDING) *sensu* AN *et al.* (1985) belongs to *P. protoanserinus* sp. n. There are no figures of *P. serrus* in FÅHRÆUS and HUNTER (1981) and FÅHRÆUS (1982). According to three pygodontiform elements from the sample CTH14 of Cottles Island section, New World Island, north-central Newfoundland, *P. serrus* (HADDING) *sensu* FÅHRÆUS *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 HÄL17.05 and HÄL18.48, see Fig. 5B).

P. protoanserinus sp. n. and *P. anserinus* occur repeatedly three times at Quarry Cove section, New World Island, north-central Newfoundland (FÅHRÆUS and HUNTER 1981: fig 2, table 1; FÅHRÆUS 1982: fig. 2). FAHRÆUS (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. BERGSTRÖM (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*? *ruedemanni* by LANDING (1976) from the early Arenig *Oepikodus evae* Zone.

LÖFGREN (1990) described in detail the platform elements of *Polonodus* and belived 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 assigment 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* LINDSTRÖM, 1957

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

Pygodus lunnensis sp. n.
(Pl. 1: 12–16; Figs 2A, 4A)

1978. *Pygodus*? sp. B; LÖFGREN: p. 97, pl. 16: 2, 3.

1983. *Pygodus*? n. sp.; BERGSTRÖM: p. 45, fig. 3.

?1987. *Polonodus tablepointensis* STOUGE; HÜNICKEN and ORTEGA: p. 140, pl. 7.1: 2 (non 1).

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)

1913. *Arabellites serra* n. sp.; HADDING: p. 33, pl. 1: 12, 13.
1955. *Periodon serra* (HADDING); LINDSTRÖM: pl. 22: 17–21, 25 (non 22–24).
1960. *Pygodus* n. sp. 2; LINDSTRÖM: p. 91, fig. 7: 1.
1961. *Pygodus anserinus* LAMONT *et* LINDSTRÖM; WOLSKA: p. 357, pl. 5: 4 (non 5).
1964. *Pygodus* sp. LINDSTRÖM; HAMAR: p. 280, pl. 4: 5–8, fig. 6: 8.
1966. *Pygodus trimontis* n. sp.; HAMAR: p. 70, pl. 7: 12, 16, 17.
1967. *Pygodus* aff. *anserinus* LAMONT *et* LINDSTRÖM; VIIRA: fig. 4: 6.
1967. *Haddingodus serra* (HADDING); VIIRA: fig. 4: 7.
1971. *Pygodus serrus* (HADDING); BERGSTRÖM: p. 149, pl. 2: 22, 23.
1974. *Pygodus serrus* (HADDING); BERGSTRÖM *et al.*: pl. 1: 18.
1978. *Pygodus serra* (HADDING); LÖFGREN: 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).
1990. *Pygodus serrus* (HADDING); AN and ZHENG: pl. 13: 11–14,17–21.
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).
1997. *Pygodus anserinus* LAMONT *et* LINDSTRÖM; ARMSTRONG: p. 776, pl. 4: only 4.

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 (LÖFGREN 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).

Comments on the synonymy list. — The pygodontiform element figured by BERGSTRÖM (1971: pl. 2: 23) is from the lower part of the Furudal Limestone, which probably corresponds to the *E. reclinatus* Subzone. One specimen figured by AN and ZHENG (1990: pl. 13: 20) occurs together with *E. reclinatus* and another (AN and ZHENG 1990: pl. 13: 21) with *E. lindstroemi*. Specimens occurring together with *E. robustus* were figured by CHEN and ZHANG (1984: pl. 2: 12, 13, 21, 22), AN (1987: pl. 26: 1, 2, 4, 5), and WOLSKA (1961: pl. 5: 4). The specimens figured by HAMAR (1966: pl. 7: 12, 16, 17), VIIRA (1967: fig. 4: 6, 7) and BERGSTRÖM *et al.* (1974: pl. 1: 18) occur together with *E. lindstroemi*. The specimens figured by DZIK (1994: pl. 17: 9–12, fig. 26) occur together with *E. robustus* and *E. lindstroemi*. The pygodontiform element figured by ARMSTRONG (1997: pl. 4: 4) is from the lower part of the *P. anserinus* Zone.

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 Hällekis 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).
1961. *Pygodus anserinus* LAMONT *et* LINDSTRÖM; WOLSKA: p. 357, pl. 5: 5 (non 4).
1966. *Pygodus anserinus* LAMONT *et* LINDSTRÖM; HAMAR: pl. 7: 1.
1976. *Pygodus serrus* (HADDING); DZIK: fig. 29a, b.
1979. *Pygodus serra* (HADDING); HARRIS *et al.*: pl. 2: 18.

1981. *Pygodus serrus* (HADDING); AN: pl. 4: 1–3.
1982. *Pygodus serrus* (HADDING); AN and DING: pl. 5: 13, 14, 16, 19, 22.
1984. *Pygodus serrus* (HADDING); CHEN and ZHANG: p. 329, pl. 2: 9–11, 18–20 (non 12, 13, 21, 22).
1985. *Pygodus serrus* (HADDING); AN *et al.*: pl. 17: 2–6.
1985. *Pygodus serra* (HADDING); BERGSTRÖM and ORCHARD: pl. 2.2: 5
1987. *Pygodus serra* (HADDING); NI and LI: pl. 59: 25.
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.
1990. *Pygodus serra* (HADDING); BERGSTRÖM: pl. 1: 23, 24.
1990. *Pygodus serra* (HADDING); POHLER and ORCHARD: pl. 1 : 18.
1991. *Pygodus serra* (HADDING); MCCRACKEN: p. 51, pl. 2: 4, 6, 7, 9, 11, 12, 14–18, 20–23, 28–30.
1991. *Pygodus* sp. cf. *P. serra* (HADDING); MCCRACKEN: p. 51, pl. 2: 1–3, 5, 8, 10, 13, 19.
1993. *Pygodus serrus* (HADDING); DING *et al.*: p. 198, pl. 30: 10, 13, 15–18, 20–22, 24, pl. 35: 24, 26.
1994. *Pygodus serra* (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 Häl 16.64, the middle of Gullhögen Limestone (Fig. 5B).

Type locality: Hällekis, 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 serra.*

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. serrus* (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 Hällekis section, Västergötland, Sweden (Fig. 5B).

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THE ORDOVICIAN CONODONT GENUS *PYGODUS*

PLATE 1

Pygodus anitae BERGSTRÖM 91

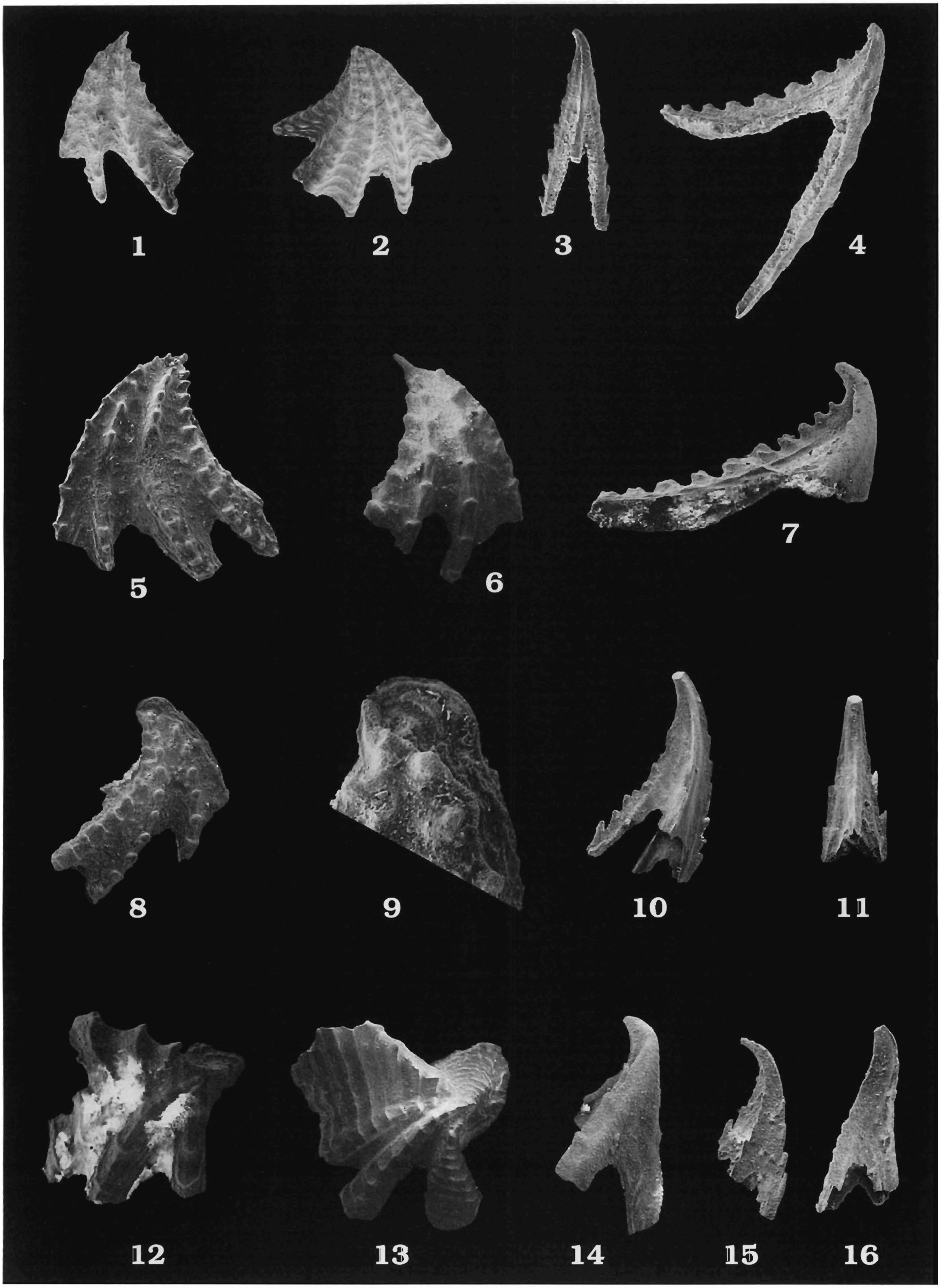
1–4 from Kullstaberg section, Jämtland, Sweden, 5–11 from Lunne quarry, Jämtland, Sweden.

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.
7. Haddingodontiform element, × 50, lateral view, sample Lu4.50, SO-9516.
8. Pygodontiform element, × 35, upper view, sample Lu3.65, SO-9508.
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. 95

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.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THE ORDOVICIAN CONODONT GENUS *PYGODUS*

PLATE 2

Pygodus serra (HADDING) 96

From Hällekis quarry, Västergötland, Sweden.

1. Pygodontiform element, × 60, upper view, sample HÄL15.95, SO-9537.
2. Pygodontiform element, × 55, upper view, sample HÄL15.95, SO-9536.
3. Haddingodontiform element, × 60, lateral view, sample HÄL15.95, SO-9538.
4. Tertiopedate element, × 70, postero-lateral view, sample HÄL15.95, SO-9540.
5. Alate element, × 80, posterior view, sample HÄL15.95, SO-9541.
6. Pygodontiform element, × 70, upper view, sample HÄL12.18, SO-9543.
7. Pygodontiform element, × 90, upper view, sample HÄL12.18, SO-9542.
8. Haddingodontiform element, × 80, lateral view, sample HÄL12.18, SO-9544.
9. Quadriramate element, × 90, lateral view, sample HÄL12.18, SO-9545.
10. Alate element, × 80, posterior view, sample HÄL12.18, SO-9546.
11. Pygodontiform element, × 80, upper view, sample HÄL11.69, SO-9548.
12. Pygodontiform element, × 80, upper view, sample HÄL11.69, SO-9549.
13. Haddingodontiform element, × 90, lateral view, sample HÄL11.69, SO-9554.
14. Pygodontiform element, × 80, upper view, sample HÄL11.69, SO-9547.

Pygodus anitae BERGSTRÖM (late form) 91

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

15. Pygodontiform element, × 68, upper view, sample Lu2.72, SO-9632.
16. Pygodontiform element, × 68, upper view, sample Lu2.72, SO-9633.
17. Haddingodontiform element, × 68, lateral view, sample Lu2.72, SO-9634.
18. Haddingodontiform element, × 68, posterior view, sample Lu2.72, SO-9635.
19. Tertiopedate element, × 68, postero-lateral view, sample Lu2.72, SO-936.
20. Alate element, × 68, posterior view, sample Lu2.72, SO-9637.

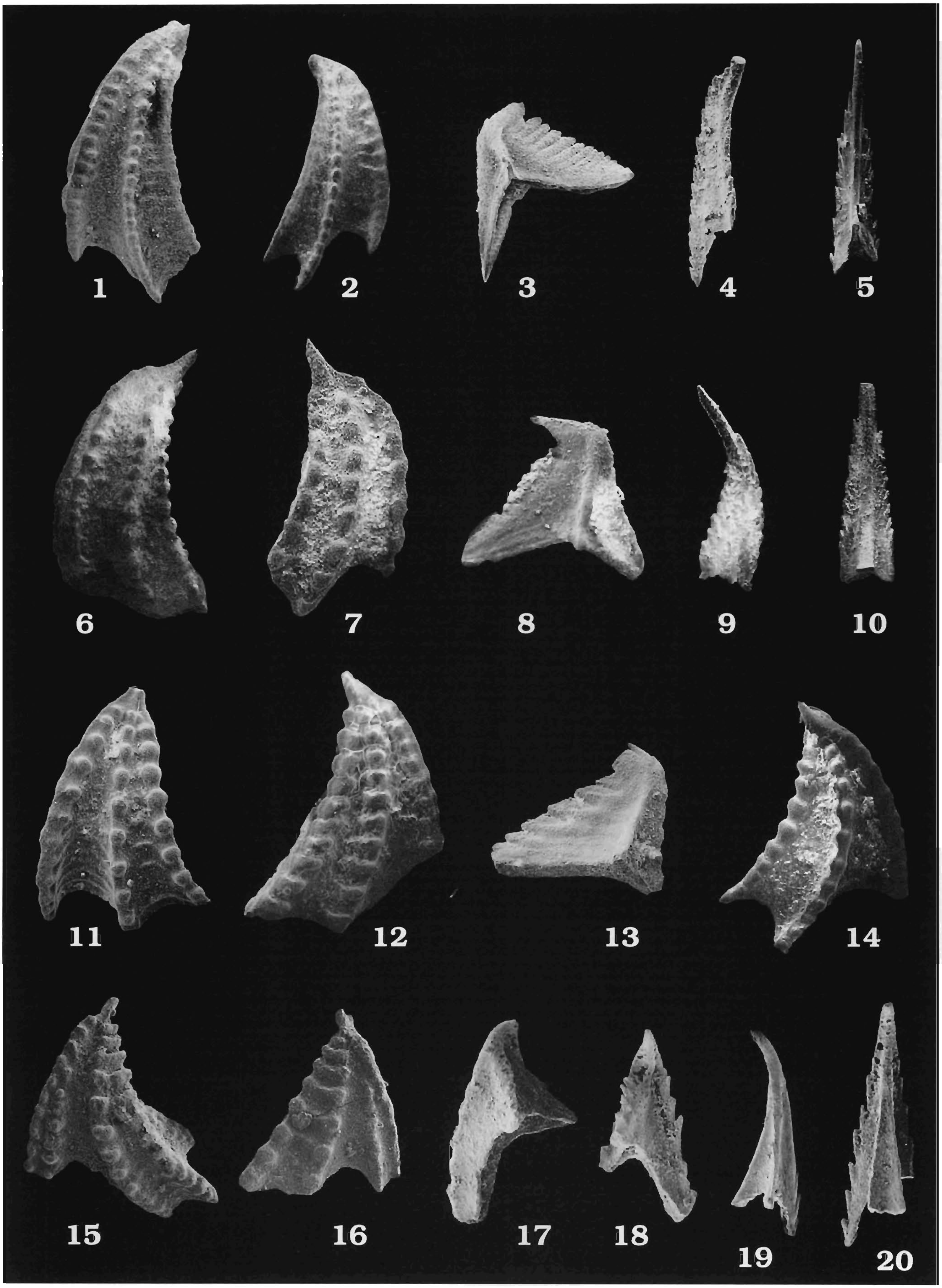
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PLATE 3

Pygodus anserinus (LAMONT *et* LINDSTRÖM) 92

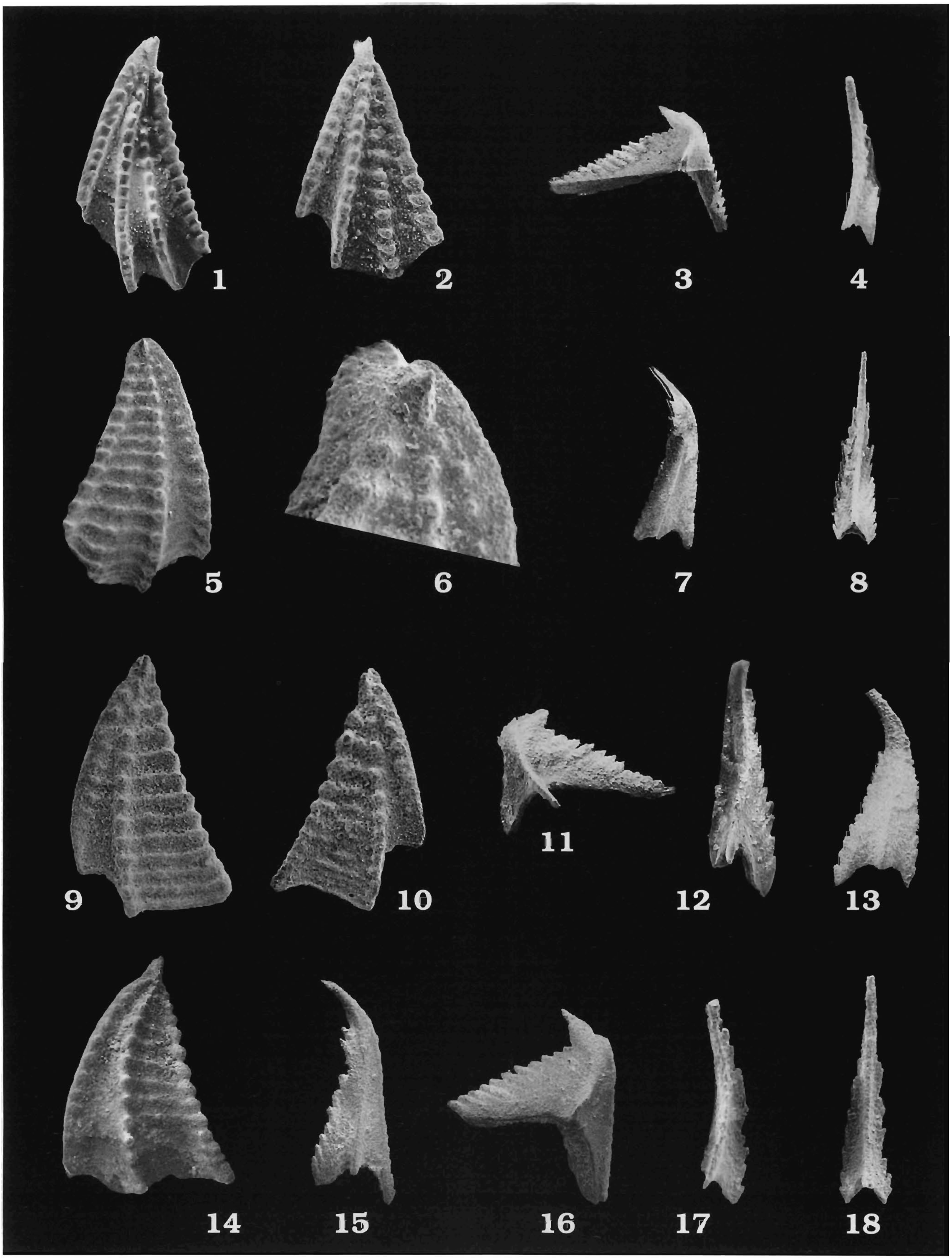
From Hällekis quarry, Västergötland, Sweden.

1. Pygodontiform element, × 55, upper view, sample HÄL20.30, SO-9519.
2. Pygodontiform element, × 55, upper view, sample HÄL19.00, SO-9522.
3. Haddingodontiform element, × 55, lateral view, sample HÄL21.11, SO-9520.
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.

9. Pygodontiform element, holotype, × 70, upper view, sample HÄL16.64, SO-9557.
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.
14. Pygodontiform element, × 70, upper view, sample HÄL12.90, SO-9531.
15. Quadriramate element, × 60, lateral view, sample HÄL12.90, SO-9533.
16. Haddingodontiform element, × 60, lateral view, sample HÄL 12.90, SO-9532.
17. Tertiopedate element, × 80, posterior view, sample HÄL12.90, SO-9534.
18. Alate element, × 80, posterior view, sample HÄL12.90, SO-9535.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