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A new large mound dwelling chiton (Mollusca), from the Late Ordovician Boda Limestone of central Sweden

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ABSTRACT

A new rare Upper Ordovician mound dwelling palaeoloricate chiton is described as *Crassaplex collicola* gen. et sp. nov. from three large isolated intermediate valves from the Katian carbonate mud mounds of the Boda Limestone in the Siljan district of central Sweden. Together with the previously known *Spicuchelodes?* sp., also from the Boda Limestone, these are the only known Late Ordovician mound dwellers so far among the palaeoloricates, adding to Ordovician environments with reported chiton remains. *Crassaplex collicola* is distinguished from other Ordovician palaeoloricate chitons by their thick and large valves that can be 2 cm in length, and especially the clear differentiation between the lateral and central valve areas.

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carbonate mud mounds;
Ordovician; Siljan district;
Sweden

Introduction

A stoutly built, new basal chiton (Mollusca) is described as *Crassaplex collicola* gen. et sp. nov. from isolated valves found in the Upper Ordovician (Katian) carbonate mud mounds of the Boda Limestone in the Siljan district of central Sweden (Fig. 1). It is a rare addition to the unusually diverse fauna of the Boda Limestone, and represents one of only two chiton taxa known from the Ordovician of Baltoscandia (Högström et al. 2009). Molluscs (e.g., cephalopods, bivalves, gastropods and rostroconchs) are otherwise the third most diverse and abundant group of the Boda Limestone (see Ebbestad & Högström 2007a for references).

Fossil polyplacophorans are generally placed in the Palaeoloricata of Bergenhayn (1955), characterised by the absence of the articulamentum layer with exposed apophyses typical of neoloricates. Vendrasco & Runnegar (2004) and Pojeta et al. (2010) regarded the Palaeoloricata as a convenient morphological grouping that most likely is paraphyletic, containing stem members of the clade Aculifera that encompass both Polyplacophora and Aplacophora (Sigwart & Sutton 2007; Smith et al. 2011; Vinther et al. 2011, 2012; Sutton & Sigwart 2012 and references in these). The aculiferan divergence may have happened in the Ordovician where palaeoloricates with a narrow morphology potentially represent stem-aplacophorans, in that they do not possess a foot, e.g. the typical creeping sole of modern chitons. Rather these stem forms have a spiculate girdle surrounding the dorsal valves and a vermiform body plan (Vinther et al. 2011; Sutton & Sigwart 2012). Two such forms from the Late Ordovician (Katian) of Scotland, *Septemchiton grayiae* (in reality *S. vermiformis*) and *Phthipodochiton thraivensis* (see Table 1), were discussed as possible stem-aplacophorans (Vinther et al. 2011; Sutton & Sigwart 2012), but assessing whether other Ordovician palaeoloricate taxa are stem-aplacophorans or stem-polyplacophorans is difficult without special preservation or

articulated specimens (see discussion in Sutton & Sigwart 2012). Thus, the position of *Crassaplex* remains unclear, although the large size (uncertain character) and thick valves (compared to the thin valves of the before mentioned forms) may suggest a polyplacophoran affinity. Support for the clade Aculifera today comes from both molecular and fossil data, for example Giribet (2014), Vinther et al. (2017) and Kocot et al. (2020).

Lower Palaeozoic palaeoloricates are rare fossils, showing diversity peaks in the Lower Ordovician and middle Silurian (Hoare & Pojeta 2006; Puchalski et al. 2008). The scant record may not signify a biological signal but rather seems to be a factor of a geographically and stratigraphically thinly spread and sporadic sampling effort (Puchalski et al. 2008). This was amply demonstrated by the study of Hoare & Pojeta (2006) from U.S.A. which alone increased the number of chitons known from the Ordovician by 42% and specifically for the Middle Ordovician by over 150%. In the case of the Boda Limestone, the sampling effort has been high since commercial quarrying started in the 1930's. In particular, Elsa Warburg and Orvar Isberg contributed during the 1920's and 1930's to the extant collections, but only one valve was found among this early material. It is significant that the new finds all are from Jutjärn quarry, which today is the only active quarry in the Boda Limestone. It has provided access to the deeper core material and fossil pockets in these, which in other quarries are long since gone. This may suggest that chiton material may be more common but is not recovered due to limited outcrop that exist for a short time only. However, the Boda Limestone mounds represent a high energy environment, where remains of organisms likely are fragmented, destroyed, and often eroded, thus becoming increasingly difficult to recognise for the non-specialist. Cherns & Wright (2000), also pointed out that chiton valves have lower preservation potential due to

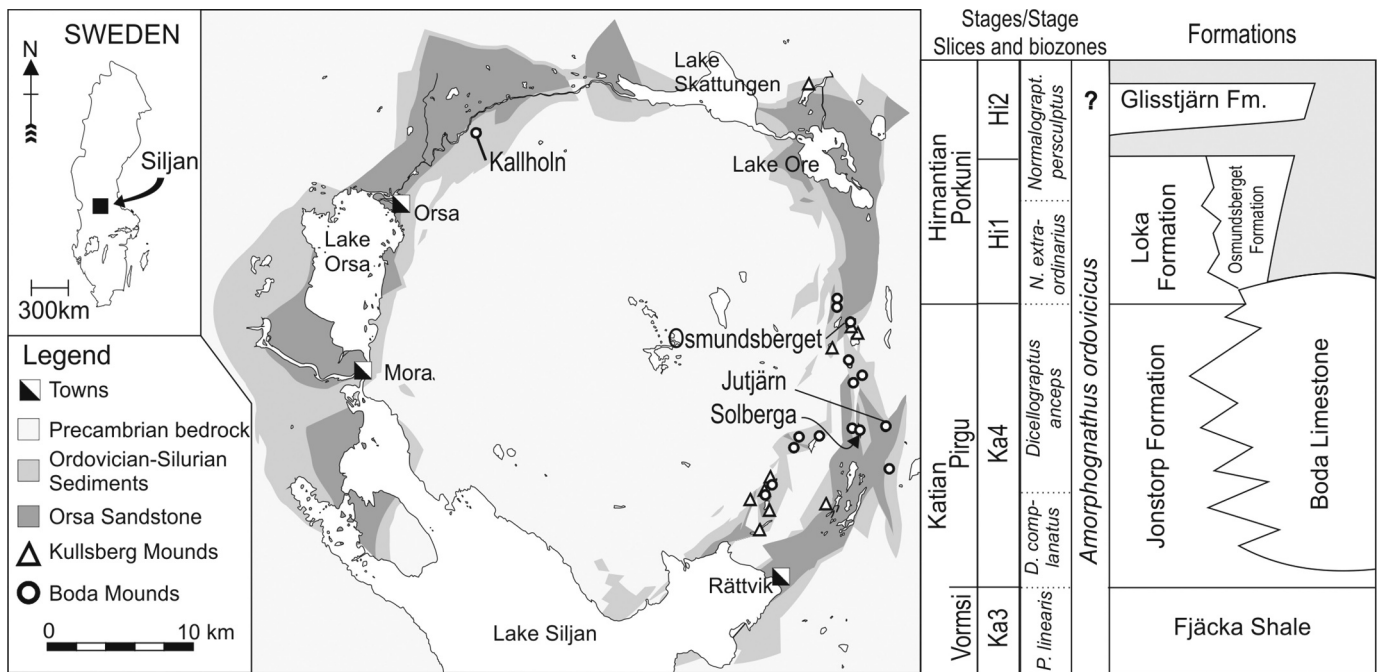


Figure 1. Map of the Siljan ring structure with the location of the older Kullberg and the younger Boda carbonate mounds and Jutjärn quarry (WGS 84 60°58'57.7"N 15° 15'3.3"E). The stratigraphical column to the right shows the global standard for stages, graptolite, and conodont biozones, in addition to the regional stratigraphy of the Siljan district, Stage Slices based on Bergström et al. (2009). Stratigraphy based on Ebbestad et al. (2015) and Kröger et al. (2016).

Table 1. Upper Ordovician – lower Silurian (Sandbian–Telychian) palaeoloricate taxa. Ordovician Stage Slices follow those defined by Bergström et al. (2009).

Taxon	Occurrence	Local stage	Stage Slice
<i>Helminthochiton griffithi</i> Salter in M'Coy, 1846	Kilbride Fm., Ireland	-	Telychian
<i>Thairoplax birhombivalvis</i> Bergenhayn, 1955	Lower Visby Fm., Sweden	-	Telychian
<i>Septemchiton vermiformis</i> Bergenhayn, 1955	South Threave Fm., Lady Burn Starfish Bed, Scotland	Rawtheyan	Ka4
<i>Crassaplex collicola</i> gen. et sp. nov.	Boda Limestone, Sweden	Pirgu	Ka4
<i>Spicuchelodes?</i> sp. Högström et al. (2009)	Boda Limestone, Sweden	Pirgu	Ka4
<i>Phthipodochiton thraivensis</i> (Reed, 1911)	South Threave Fm., Lady Burn Starfish Bed, Scotland	Rawtheyan	Ka4
<i>Septemchiton iowensis</i> (Rhoads, 1962)	Maquoketa Fm., USA	Richmondian	Ka2
<i>Chelodes</i> sp. sensu Dzik, (1994)	Upper Mójcza Lst., Poland	Nabala	Ka2
<i>Bursata santacruensis</i> (Dzik, 1994)	Upper Mójcza Lst., Poland	Haljala–Nabala	Sa2–Ka2
<i>Sarkachiton kielcensis</i> Dzik, 1994	Upper Mójcza Lst., Poland	Haljala–Nabala	Sa2–Ka2
<i>Priscochiton?</i> sp. sensu Dzik (1994)	Upper Mójcza Lst., Poland	Haljala–Nabala	Sa2–Ka2
Paleoloricate gen et sp. nov. Candela et al. (2014)	Kirkcolm Fm., Scotland	Cheneyan	Ka1
<i>Helminthochiton blacki</i> Hoare & Pojeta, 2006	Lexington Lst., Curdsville Lst. & Grier Lst. Mbrs, USA	Chatfieldian	Ka1
<i>Listrochiton weiri</i> Hoare & Pojeta, 2006	Lexington Lst., Perryville Lst., Grier Lst. & Devils Hollow mbrs, USA	Chatfieldian	Ka1
<i>Alastega martini</i> Hoare & Pojeta, 2006	Lexington Lst., Perryville Lst. Mbr., USA	Chatfieldian	Ka1
<i>Preacanthochiton baueri</i> Hoare & Pojeta, 2006	Grand Detour Fm., Forreton Mbr., USA	Turinian	Sa2
<i>Echinochiton dufoei</i> Pojeta et al., 2003	Grand Detour Fm., Forreton Mbr., USA	Turinian	Sa2
<i>Helminthochiton marginatus</i> Hoare & Pojeta, 2006	Grand Detour Fm., Forreton Mbr., USA	Turinian	Sa2
<i>Septemchiton grayiae</i> (Woodward, 1885)	Balclatchie Fm., Laggan Mbr., Scotland	Burellian	Sa2
<i>Solenocaris solenoides</i> Young & Young, 1868	Balclatchie Fm., Bellmore & Pumphouse mbrs., Scotland	Burellian	Sa2

disarticulation and aragonitic dissolution. Additionally, a recent study by Peebles & Smith (2019) suggested that dissolution before burial can be enough to remove chiton remains from the fossil record over time. In some instances, chitons are very common in localized facies, such as *Solenocaris solenoides* Young & Young, 1868 in the Ordovician of Girvan, Scotland (Stewart & Owen 2008).

Due to the sparse records and a few geographically specific monographic studies, the geographical distribution of Ordovician chitons is biased towards northern and marginal Laurentia (e.g. U.S.A., Ireland, Scotland) and for the Silurian towards Baltica (e.g. Gotland) (see for example Bergenhayn 1955; Candela et al. 2014; Cherns 1998a, 1998b, 2004; Hoare & Pojeta 2006; Sigwart 2007;

Sutton & Sigwart 2012; Vendrasco & Runnegar 2004). While Palaeozoic chitons are known from a range of depositional settings, *Crassaplex* and *Spicuchelodes?* sp. from the Boda Limestone are the only known carbonate mound dwellers (Table 1).

The inferred large size of *Crassaplex* individuals reflects the distribution of other large benthos in the Boda Limestone. Kröger (2013) and Kröger & Ebbestad (2014) showed that the diverse cephalopod fauna with 61 species known represent the top predators in the trophic structure of the Boda mounds. Large species of trilobites, bivalves and some brachiopods are among the dominating elements of the benthos, to which the large *Crassaplex* can be added. These were probably important prey for the abundant cephalopods.

Geological setting and material

The Boda Limestone of the Siljan district, central Sweden, comprises large carbonate mud mounds showing no organic frame work. The structures may reach a diameter of up to 1000 m with a thickness of 100–140 m, and are well exposed in a number of quarries (Ebbestad & Högström 2007b). The core consists of dense micrites replaced laterally by pelmatozoan flank facies. These two are Katian in age, while a terminal bioclastic facies, the Osmundsberget Formation, is entirely Hirnantian (Suzuki et al. 2009; Rasmussen et al. 2010; Kröger et al. 2016). The depositional environment seems to represent cool, nutrient rich water in the deeper neritic zone with a depth of 100–140 m (Kröger & Ebbestad 2014).

Synsedimentary and early postdepositional vertical fissures of variable size and development are characteristic for the core facies (referred to as pockets by Suzuki & Bergström 1999). The fissures are arranged radially or circumferential along the mounds and display complex morphologies and depositional history (Kröger et al. 2015, 2016). Fissures are often filled with a coquina of one of nine common trilobites interspersed with other fossil groups as a minor component. Typically, the faunal elements trapped in the fissures would live on the top surface of the mounds, being mostly transported into their resting place (Suzuki & Bergström 1999). Macrofossils are uncommon in the micritic facies. A plethora of trilobites, brachiopods, echinoderms, molluscs and corals are described from the Boda Limestone (see references in Ebbestad & Högström 2007a; Kröger 2013), but many of the molluscan groups are still in great need of descriptive work and revision.

Three intermediate valves of the herein described *Crassaplex* are known, all collected from the Jutjärn quarry in Dalarna. They are stored at the Museum of Evolution, Uppsala University, Uppsala, Sweden (PMU). Specimen PMU 25141 was found in a fissure filling dominated by *Stenopareia oviformis* (Warburg, 1925) excavated from the deepest part of the quarry in 2005. Other associated taxa are the trilobites *Eobronteus laticauda* (Wahlenberg, 1818) and *Sphaerexochus calvus* M'Coy, 1846, as well as the gastropod *Cataschisma microsoma* (Koken in Koken & Perner, 1925). The other two valves, PMU 26954 and PMU 26955, were collected 2009 and the former is also associated with *Stenopareia oviformis*. It is therefore likely that the fossils are from contemporaneous deposits. Only the intermediate valves are known.

Terminology of polyplacophorans and parameters for standard measurements follow that of Cherns (1998a). The term valve has been used for polyplacophorans to a larger extent than sclerite as used by Högström et al. (2009); here we use the term valve.

Systematic palaeontology

PHYLUM MOLLUSCA LINNAEUS, 1758

PALAEOLORICATA BERGENHAYN, 1955

Remarks. Following the discussion in especially Sutton and Sigwart (2012) we see it fit to regard Palaeoloricata as an unresolved clade containing genera that may belong to the

stem group Aculifera, the Polyplacophora and/or the Aplacophora.

Genus. *Crassaplex* gen. nov

Type species. *Crassaplex collicola* sp. nov from the Katian Boda Limestone of the Siljan district, Dalarna, Sweden.

Diagnosis. As for type species.

Etymology. From Latin *Crassus* for thick or stout and *plax* from the Greek word for plate. The gender is feminine.

Remarks. Specimen PMU 25141 was described as *Chelodes* sp. A by Högström et al. (2009). However, *Chelodes* as understood today is morphologically widely defined, as well as a long ranging genus (for example, Lower Ordovician – upper Silurian/Lower Devonian stated by Cherns 1998a, and late Cambrian – Early Devonian stated by; Pojeta et al. 2003), with a global distribution. It does seem as the current understanding of *Chelodes* requires a thorough examination and redefinition but this is outside our scope here. *Crassaplex* distinguishes itself from *Chelodes* primarily in the highly arched, roughly squarish valves compared to the often substantially elongated *Chelodes* ones, and the sharp distinction between central and lateral valve areas. Comparing median length/length ratios (Table 2) for *Crassaplex* with those of different *Chelodes* taxa described in Cherns (1998a) give similar results, although the ratio may be somewhat lower in *Crassaplex* compared to that of *Chelodes*. Although not always present in *Chelodes*, granulated ornamentation as described by Cherns (1998a) is seemingly missing in the Boda Limestone taxon. Additionally, *Crassaplex* exhibit central and lateral valve areas that are very distinctly separated in a manner not seen in most *Chelodes* taxa, Cherns (1998a) indicated that in this genus the valve areas are lacking or weakly expressed, although a few cases are more well-defined. *Preacanthochiton* Bergenhayn, 1960 share similarities with *Crassaplex* in the overall shape of valves but differ primarily in the weaker differentiation of medial and lateral valve areas, as *Chelodes* does.

Crassaplex collicola sp. nov.

Figure 2A–L, Table 2

2009 *Chelodes* sp. A. Högström, Ebbestad & Suzuki, fig. 5A–F.

Table 2. Measurements for the three described plates of *Crassaplex collicola* gen. et sp. nov., terminology and measurements after Cherns (1998a). The apical angle in specimen PMU 26954 is an estimate, as the posterior-lateral margins are not well preserved.

	PMU 26954	PMU 26955	PMU 25141
Length mm	>15	>12	>19.5
Median length mm	14.6	>11.5	>17.3
Width mm	–	–	~20
Height mm	–	0.4	10
Central valve area mm	–	–	12.5
Lateral valve area mm	–	–	7.3
Apical angle	~66°	–	105°
Jugal angle	103°	106°	98°
Median length/Length	>0.97	~0.96	~0.89

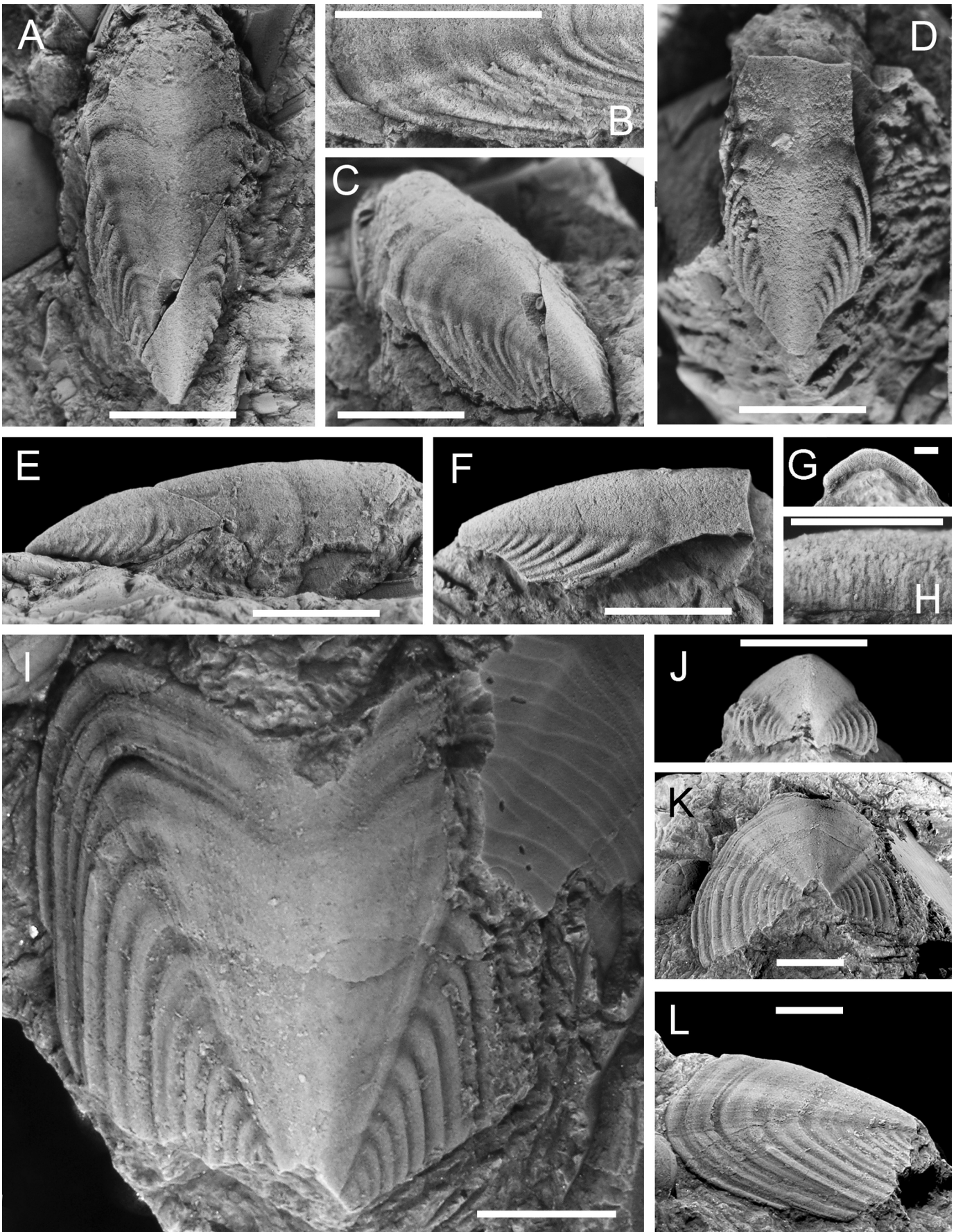


Figure 2. A–L. *Crassaplex collicola* n. gen., n. sp. A–C, E. PMU 26954, dorsal, detail of lateral valve area, dorsal oblique, and lateral views respectively. The lateral margins are largely missing D, F–H, J. PMU 26955, dorsal, lateral, anterior and cross section of anterior margin respectively. The lateral margins are largely missing I, K–L. PMU 25141, Holotype and most complete specimen. All specimens from Jutjärn quarry. PMU 25141, coll., J.O.R. Ebbestad, 2005; PMU 26954, 26955, coll. J. Suzuki, 2009. Scale bar in A–F, I–L = 0.5 cm; scale bar in G, H = 0.1 cm.

Material. Three isolated intermediate valves from Jutjärn quarry (Fig. 1), Upper Ordovician (Katian) Boda Limestone, the Siljan district, Dalarna, Sweden. Measurements are given in Table 2.

Holotype. PMU 25141, Fig. 2E, K, L.

Etymology. The species epithet *collicola* means Mound Dweller. From Latin *Collis* meaning hill or mound, and New Latin *Colus* meaning dweller.

Diagnosis. Intermediate valves thick and can reach a large size. Shell with distinct embayment, and comarginal rugae on lateral valve area, Ridges absent on highly arched central valve area. Jugal angle around 100°. Slightly beaked but sharp apex with a general squarish appearance of valves in dorsal view.

Description. Large (2 cm in length), robust valves, ventral surface not exposed. Central valve area large and essentially without ornamentation except for faint traces of the comarginal rugae near the anterior margin, rugae running nearly straight (antero-posteriorly) on the lateral valve areas. Conspicuous anterior embayment clearly visible in specimens PMU 26954 and PMU 25141, highly arched valve, and sharply marked line between central and lateral valve areas. PMU 25141 roughly square in dorsal view. PMU 26954 (Fig. 2, A–C, E) has broken lateral margins, partially preserved anterior margin with distinct embayment, apical region nearly intact showing pointed slightly beaked apex, the valve is cracked. PMU 26955 (Fig. 2, D, F–H, J) has no preserved complete margin but apical region nearly complete and very similar to PMU 26954, these two also of equal size. PMU 25141 (Fig. 2, I, K–L) exposes a nearly complete anterior margin with prominent embayment and large lateral valve areas whereas the apical region is not preserved. See also Fig. 3 for a schematic illustration of valve arrangement, including inferred pointed apices.

Remarks. There is a clear difference between the two listed apical angle values for specimens PMU 25141 and 26954, likely depending on differential preservation of the posterolateral portions of the lateral margins. The two smaller specimens therefore do not preserve the squarish outline seen in the more complete specimen. The two smaller valves have no complete margins and exact measurements of the apical angle is therefore difficult, but there is a good match in general appearance between the three specimens. The median length/length ratio (see Table 2), is a rough estimate of the extent of the embayment in this taxon and the correspondence of the three values is a clear indication of their similar morphology.

Crassaplex collicola is a large taxon where a complete specimen may have reached a length of 15–20 cm (Fig. 3). The intermediate valves of *Crassaplex* are comparable in size to those of *Preacanthochiton baueri* Hoare and Pojeta (2006), an Ordovician taxon from U.S.A. with valves of broadly similar shape, faint ridges on the lateral valve areas and an embayment of similar extent compared to the Boda Limestone taxon, but



Figure 3. Schematic illustration of *Crassaplex collicola*, head and tail valves are unknown, and in this illustration represented by stippled markings. The outline of the body is conjectural, and the presence/absence of a foot is unknown. Scale bar = 1 cm.

consistently described as possessing thinner valves. Some of the larger individuals of *Chelodes* from the Silurian of Gotland may have reached a total length of around 10 cm (Cherns 1998a), but far from all *Chelodes* were that large.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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