Polychaete jaws

CLAES BERGMAN

There are very few previous reports of polychaete jaws (scolecodonts) from the Silurian of Gotland. Although, according to Hinde (1882:4) and Thorell & Lindström (1885:4), Angelin had identified specimens from Gotland as jaw elements of annelids as early as 1864, the paper by Hinde (1882) is the first published account of these fossils from the island. Hinde's report is a well illustrated account of scolecodonts from two localities, one of which was in "decomposed shale from the neighbourhood of Wisby", later stated by Thorell & Lindström (1885:4) to be from the "*Pterygotus*" Beds of Vattenfallet.

Hede recorded the occurrence of annelid jaws from a large number of localities on Gotland in the descriptions of the geological map sheets. More recently Martinsson (1960) described two clusters of jaws from the Mulde Marl, and Eisenack (1975) discussed some scolecodont material from the island within a more general study of the group.

I am currently studying both fused and dispersed polychaete jaws from the Silurian of Sweden, mainly from Gotland. A full discussion of the taxa tentatively identified here is in preparation. Specimens have been picked from the same residues as those prepared for conodont extraction. For further information on the samples and their treatment, see Jeppsson (this volume). 13,581 jaw elements from Vattenfallet have been examined, but only a few of these were fused. 16 separate species are distinguished (Fig. 26), 10 of which were not described by Hinde (1882). He named 26 different species from about 1 kg of soft "*Pterygotus*" marl, but in my opinion about 20 of these are synonyms.

Taxonomy, nomenclature and terminology

Various authors have proposed that a parataxonomic system should be used for disaggregated jaw elements and that clusters should be named separately. A proposal of this kind by Moore & Sylvester-Bradley (1957) was rejected by the 15th International Congress of Zoology in 1958 (Kielan-Jaworowska 1968), and thus the only valid nomenclatorial basis is that which follows current I.C.Z.N. rules (e.g. article 23). Similar problems have been widely discussed with regard to conodonts, and the success in attempting to apply strictly biological criteria for taxonomy suggests that the same success can be achieved for polychaetes.

In this study I have mainly used the morphology of the first maxillae (MI) to distinguish different species, although some of the other jaw elements of each



Fig. 26.





- ◎ "Lumbriconereites" "obliquus" (n MI/kg)
- × Eunicites serrula (nM/kg)
- Δ Arabellites contractus Remaining species (10)
 - □ Oenonites? sp.a
- "Lumbriconereites" spatiosus
 "Lumbriconereites" "obliguus"
- Oenonites aspersus
- × Eunicites serrula (note that this curve is reversed relative to the others)

species have also been identified using the same methods as those employed in reconstructing conodont apparatuses. Further work is required to identify the remaining jaw elements of these species.

I have not yet studied the type specimens of the species involved, and thus it is impossible at this stage to determine which of the many names used for single jaw elements has priority. Since the elements in my samples from the "Pterygotus" Beds can be compared easily with those figured in Hinde's (1882) paper, I have tentatively used his names where possible. As this is one of the oldest papers on scolecodonts it is reasonable to assume that most of Hinde's species names have priority, although some of the generic names that he used (Hinde 1879, 1880, 1882) will probably be replaced by others when full taxonomic revisions are made.

Descriptive terms used here are those in the "glossary of descriptive terms" of Jansonius & Craig (1971:257). I use 'cluster' in the sense of Pollock (1969:929) rather than 'assemblage' since the latter has been used with different meanings by different authors.

Annotated faunal list

Arabellites contractus Hinde, 1880 (Fig. 28:2A–B); A. fastigiatus Hinde, 1882 (Fig. 28:1A–B). The type species of Arabellites Hinde, 1879, is A. hamatus Hinde, 1879, and according to Hinde (1880, 1882) the two species here identified from Vattenfallet are congeneric. However, there may be some doubt as to whether both contractus and fastigiatus should be included in this genus. At present MII and MIV of Arabellites can not be identified at the species level and they are here referred to as A. sp. indet.

Kozlowskiprion? sp. a (Fig. 28:9). The MI of this species are similar to those of K. longicavernosus described by Kielan-Jaworowska (1966:98).

"Lumbriconereites" "obliquus" (Eichwald, 1854) (Fig. 28:7A-C). It is doubtful whether Hinde was correct in placing this species in the genus Lumbriconereites, and whether he correctly identified specimens with those of Eichwald's species. The jaws of the type specimen of the type species of Lumbriconereites Ehlers, 1868 are poorly preserved (Jansonius & Craig 1971:273), making a comparison between them and the specimens described by Hinde very difficult. The specific name obliquus Pander, 1856 was used by

Fig. 27. Absolute and relative frequencies of jawed polychaete species at Vattenfallet. Adjacent samples having a low absolute frequency have been grouped together. The data are based on counts of MI except for *Eunicites* and Gen. et sp. indet. b and c, for which all maxillae have been counted. In B, C and D, samples containing less than 35 specimens have been grouped with the nearest sample below or above.

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SGU 2628-2637 500 6	3 1	-	1 –	-	•	-	-	-	-	-	1 -	- ·		-	-	-	-	-	
SGU 25.6-25.8 270 26	7 –	-	3 -	-	-	-	-	-	-	-		-		-	-	-	-	-	
SGU 24.6-24.7 145 979	142 7	2	15 20	1	4	4	3	1	1	27	-	1	- 2	3	-	-	-	3	
SGU 23.70 285 393	112 7	2	13 17	3	2	2	-	3	2	17	-	5 .		1	-	-	-	-	
SGU 22.90 195 677	132 2	8	18 25	4	2	1	1	3	-	20		-	1 –	3	-	-	2	-	
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SGU 20.9-21.4 180 339	61 5	3	37	2	1	-	1	-	-	10	-	1	- 1	3	-	-	1	-	
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G70-7 LJ 14.38-14.48 500 366	183 4	10	5 10	6	8	-	1	2	-	78	1 .	-	- 5	3	1	-	-	-	
G 70-8 LJ 13.33 2500 352	879 23	22	63 65	15	25	9	10	9	1	309	6	5	5 5	23	3	-	9	13	
G 70-9 LJ 12:38-12:43 500 50	25 1	-	- 2	2	1	-	-	1	-	-		-	-	-	-	-	1	-	
G 70-21 LJ 11.20-11.23 2500 44	110 1	4	4 7	1	1	2	-	1	-	46	- °	1		2	-		2	1	
G 70-20 LJ 10.02-10.04 3670 112	412 17	21	19 24	6	9	6	6	8	-	121	12	8	8 19	-	-	-	5	7	
G 70-22 LJ 8.94 500 40	20 1	1	1 1	-	4	-	-	-	-	5	- 1	1	1 2	-	-	-	-	-	
G 70-19 LJ 6.49-6.54 500 40	20 1	-	1 4	-	-	-	-	-	-	6		-	- 12	-	-	-	-	-	
G 70-18 LJ 5.59 500 48	24 1	-	3 3	-	1	-	-	1	+	-		-	1 -	-	-	-	-	-	
G 70-17 LJ 4.26-4.33 500 46	23 2	-	2 1	-	1			1	-	3	2	1		· -		-	1	1	
G 70-16 LJ 3.06-3.16 500 48	24 3	1		1	1	-	1	1	-	5	1	-	- 334	- 4	1	-	-	-	
G 76-8 LJ 2.58-2.62 2000 100	199 10	6	1 2	6	8	2	2	2	-	57	2	7	1.07	8	1	-	6	6	
G 70-15 LJ 1.86-1.96 1300 75	98 9	3	2 2	-	2	2	-	-	-	10	11 1	0		1	1	-	-	-	
G 76-7 LJ 1.73-1.78 2000 19	37 2	4	- 1	-	-		-	-		12	1	1		- 3	-	1	-	-	
G 70-14 LJ 0.99-1.06 840 142	119 10	13	1 -	1	1	3	2	-	-	23	3	7	-	4	-	1	-	-	
G 76-6 LJ 0.94-0.99 2000 184	368 31	24	4 12	1	5	1	2	1	2	60	4	3 1	21 25	5 9	-		- 76	-	

TABLE 2. Frequencies of various polychaete jaw elements in the samples from Vattenfallet. The sample "Valdaria RM" was processed at the Riksmuseum and the other samples by L. Jeppsson. Abbreviations in sample numbers: RM=Riksmuseum; SGU=Geological Survey of Sweden (Liljevall's samples); LJ=L. Jeppsson, Lund. Note the small sample weight in some samples from Högklint b and c.

Gen. et sp.indet. c	Gen. et sp.indet b	Eunicites sp. a	Arabellites	Krabellites fastigiatus "Lumbrico - nereites" spatiosus						Gen.et sp.indet.d	Oenonites?spa		Xanioprion sp.a	<i>Oenonites</i> sp. indet.			Arabellites sp indet.			Sp. a		Gen. et sp. indet.			Mandibel sp. indet.		Anterior and
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-	-	-	2	2	93	94	11	6	-	-	51	44	-	66	51	-	1	_	_	-	-	54	59	53	17	2	- 13
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Hinde without having studied the type material. Therefore I use "L." "obliquus" only as a tentative name. The possibility that some of the MII, MIV, basal plates, and carriers which I include here might belong to other species cannot be excluded.

"Lumbriconereites" spatiosus Hinde, 1882 (Fig. 28:10A-B).

Oenonites aspersus Hinde, 1879 (Fig. 28:4A–F). Hinde referred the MI of this species to O. aspersus and the MII to Arabellites anglicus. As both species names were published in the same paper either may be used and I provisionally use the name that was based on the MI. Lange (1947) noted that the MI of O. aspersus were similar to those of the specimens he named Paulinites paranaensis. Two clusters from Gotland were described by Martinsson (1960) as strikingly similar to the MI and MII of P. paranaensis. In my opinion the clusters described by Martinsson as P. burgensis are even more closely related to O. aspersus than to P. paranaensis. In fact, P. burgensis and O. aspersus may well be conspecific. So far I have not been able to distinguish the MII and carriers of O. aspersus from those belonging to Oenonites? sp. a, so I have therefore referred all these elements of Oenonites to O. sp. indet.

Oenonites? sp. a (Fig. 28:3A–B). The MI show a slight similarity to the illustrations of the MI of Arabellites hamatus Hinde (1879, Pl. 18:12; 1882, Pl. 2:42–44).

Paranereites sp. The MI of this species are somewhat similar to those figured by Eisenack (1939:168, Fig. 13) as *Paranereites*.

Ramphoprion sp. (Fig. 28:8A–C). The left MI (Fig. 28:8C) is similar to that of *Ramphoprion* sp. b of Kielan-Jaworowska (1966:11).

Eunicites serrula (Hinde, 1880) (Figs. 28:5–6). This name is used here for a group of jaws of which some are similar to those figured by Hinde (1880, Pl.

Fig. 28. All figures are SEM photographs of specimens from Vattenfallet. Specimen numbers preceded by LO refer to the collections of the Department of Historical Geology and Palaontology, University of Lund, and those by An to collections of the Section of Palaeozoology, Swedish Museum of Natural History, Stockholm. All specimens from the "Pterygotus" Beds (29.0-30.0 m) are from a Riksmuseum sample crowded with Valdaria testudo. 1. Arabellites fastigiatus: A, left MI, ×60, 29.6–30.0 m, An 2644; B, right MI, ×60, 29.6–30.0 m, An 2645. 2. Arabellites contractus: A, left MI, ×60, 29.6-30.0 m, An 2646; B, right MI, ×60, 29.6-30.0 m, An 2647. 3. Oenonites? sp. a: A, left MI, ×37, 29.6–30.0 m, An 2648; B, right MI, ×45, 29.6–30.0 m, An 2649. 4. Oenonites aspersus: A, left MI, ×45, Sample G70-10 L.J. (13.33 m), LO 5082; B, right MI, X30, 29.6-30.0 m, An 2650; C, left MI, ×45, 29.6–30.0 m, An 2651; D, right MI, ×45, 29.6–30.0 m, An 2652; E, left MI, ×45, 29.6–30.0 m, An 2653; F, right MI, ×45, 29.6–30.0 m, An 2654. 5. Eunicites serrula, M?, ×30, Sample G70-20 L.J. (10.02-10.04) m, LO 5083. 6. *Eunicites serrula*: M?, ×30. Sample G70-20 L.J. (10.02-10.04 m), LO 5084. 7. "*Lumbriconereites*" "obliquus": A, left MI, ×40, 29.6-30.0 m, An 2655; B, right MI, ×50, 29.6-30.0 m, An 2656; C, left MI, ×150, Sample G70-20 L.J. (10.02–10.04 m), LO 5085. 8. *Ramphoprion* sp.: A, left MI, ×55, Sample G70–20 L.J. (10.02–10.04 m). LO 5086; B, right MI, ×75, Sample G70–20 L.J. (10.02–10.04 m), LO 5087; C, left MI, \times 90, Sample G70-20 L.J. (10.02-10.04 m) LO5088. 9. Kozlowskiprion? sp., left MI, \times 60, Sample G70-20 L.J. (10.02-10.04 m), LO 5089. 10. "Lumbriconereites" spatiosus: A, left MI, ×45, 29.6-30.0 m, An 2657; B, right MI, ×45, 29.6-30.0 m, An 2658. 11. Gen. et sp. indet. a: A, left MI, ×60, Sample G70-8 L.J. (13.33 m), LO 5090; B, right MI, ×15, 29.6-30.0 m, An 2659.

14:18–20; 1882, Pl. 1:11,12). Some of the jaws designated as MIV without any generic and specific name might also belong to *E. serrula*.

Eunicites sp. a. The jaws resemble those figured by Kielan-Jaworowska (1966:62) as *Pristioprion* sp. b.

Xanioprion sp. One basal plate is similar to the specimen figured by Szaniawski (1970, Pl. 4:2) as X. borealis Kielan-Jaworowska, 1962.

Gen. et sp. indet. a (Fig. 28:11A–B). Only the MI are as yet identified. They are somewhat similar to "L." "obliquus" but differ in having a more prominent fang which forms a hook.

Gen. et sp. indet. b. Only two MI were found.

Gen. et sp. indet. c. The one jaw element found is somewhat comparable with that discussed and figured by Kielan-Jaworowska (1966:117, Pl. 15:1c-d) as *Kalloprion* sp. a.

Gen. et sp. indet. d. Three jaw elements (MI?) resemble the one figured by Stauffer (1933:1200) as *Paleonereites*.

Basal plates? sp. a. Under this designation I include elements that are presumably basal plates of one species, probably one of those listed above.

MIII?. Jaw elements that might be MIII from several species.

MIV. Most of these jaw elements probably belong to Eunicites serrula.

M?, Gen. et sp. indet. Specimens that have neither been identified taxonomically nor assigned to a type of element. The elements are of the same type and they all belong to the same species.

Mandibles. Three different types have been found. A, similar to those figured by Eisenack (1939:169) as *Palaeosigma*. B, similar to those figured by Stauffer (1933:1205) as *Northrites*. C, resembling *Northrites* but more slender.

Anterior and lateral teeth. A general "wastebasket" group in which different indeterminate anterior and lateral elements have been placed.

Eight clusters were found in the material from the section, of which seven, with two or four elements fused, are from Högklint b. Five of the clusters are identified as *O. aspersus* and the others as *A. fastigiatus* and "*L. obliquus*", respectively. A single cluster found on a bedding plane in the "*Pterygotus*" Beds by Lindström is referred to "*L*." "obliquus". The nine elements in this cluster are not fused.

Discussion

The abundance of polychaete jaws in the Upper Visby Marl and Högklint a is relatively low, between 10 to 100 MI/kg (Fig. 27: A), and this low abundance is coupled with a fairly low taxonomic diversity (Fig. 26). There is a pronounced increase in abundance in Högklint b, where it varies from 125 to 968 MI/kg (Fig. 27: A). This high figure might not be a reflection only of the shallower

water depths, since variation in abundance can also depend on differences in the rate of sedimentation. Högklint c shows a high variation in abundance, from 6 to 540 MI/kg. The taxonomic diversity is somewhat lower than in Högklint b. Högklint d ("*Pterygotus*" Beds) shows a variation in abundance from 140 to 1200 MI/kg.

The relative frequencies of various species is shown in Fig. 27 D. Data on Eunicites serrula may be incomplete because its jaw apparatus may include elements additional to MI, making a comparison between this and the other species somewhat tenuous. In order to distinguish the *E. serrula* curve easily from those of the other species, it has been drawn reversed. "Lumbriconereites" "obliguus" and Eunicites serrula are the most abundant taxa in the section (Fig. 27A), forming together 40 to 80 per cent of the total counts. It is interesting to note that the curves of these two species show a conspicuous correlation in that they change almost simultaneously and with about the same magnitude. This might indicate that the variation in absolute frequency reflects variations in the rate of deposition. The relative frequency curve of "L." "obliguus" is roughly reversed in comparison with that of Oenonites aspersus (Fig. 27D). The relative frequency of Arabellites contractus (Fig. 27B) is lower in the Högklint Beds than in the Upper Visby Marl and it thus appears that this species is relatively more common in deep water deposits than those of shallower water environments.

It is not always appreciated that the polychaetes represented by the jaw elements were large animals. In some modern nereid species the body of a complete individual is 20 to 50 times longer than its MI (Forney 1974). At Vattenfallet the largest MI element found belongs to "Lumbriconereites" "obliquus" and is about 9 mm long. The complete animal may have had a body length of up to half a metre.

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