

UPPER ORDOVICIAN CONODONTS FROM THE KALKBANK LIMESTONE OF THURINGIA, GERMANY

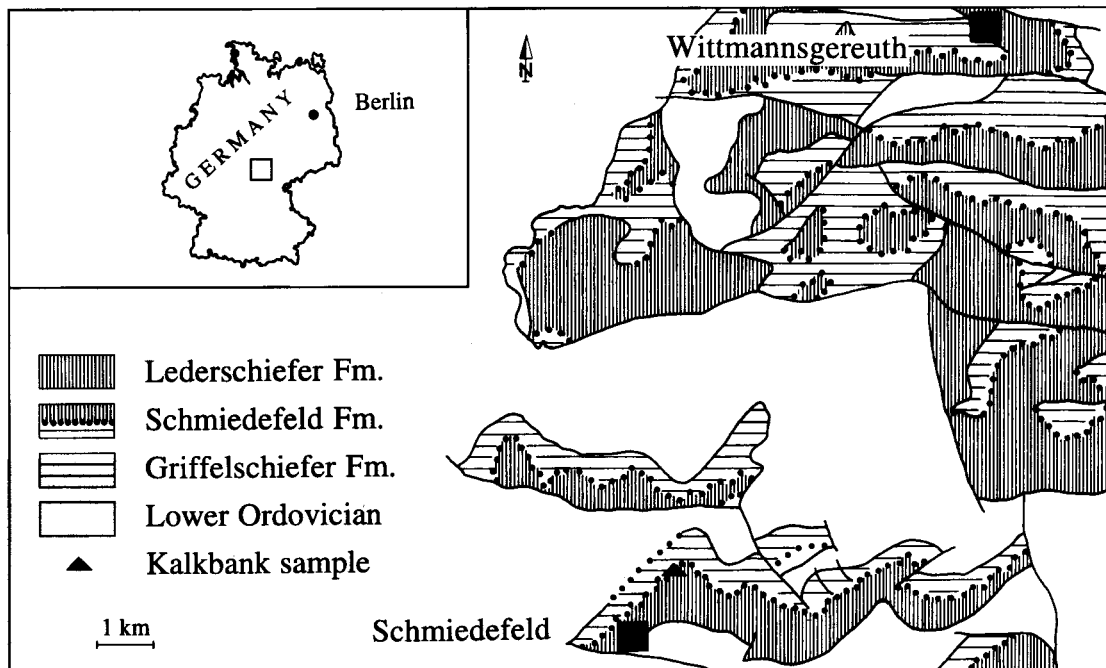
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ABSTRACT. The Kalkbank limestone of Thuringia, Germany, occurs within a condensed clastic-oolitic sequence lying below deposits associated with the Hirnantian (Ashgill) glaciation. Conodonts were first reported from this unit by Knüpfner in 1967 but described only as morphospecies. On the basis of a new collection of over 25000 specimens, 13 species belonging to 11 genera are described. The discovery of M elements of *Amorphognathus ordovicicus* and *A. ventilatus* sp. nov. indicates an early Ashgill age for this limestone. *Sagittodontina robusta*, *Scabbardella altipes* and *Istorinus erectus* are the most abundant species; *Hamarodus europaeus* is also well represented. Taxonomic revisions are made for the first two species. The conodont fauna has a Mediterranean Province affinity and shows close relations with those from the Ashgill of Spain, France and Libya and, to a lesser extent, of the Carnic Alps and Sardinia.

THURINGIA is one of the northernmost areas of Europe considered to have been part of the cold-water Mediterranean Province in the late Ordovician (Hamman *et al.* 1982; Sweet and Bergström 1984). This province has long been recognized for several different fossil groups, such as trilobites (Whittington and Hughes 1972; Cocks and Fortey 1988), brachiopods (Havlíček 1976), acritarchs (Vavrdová 1974; Martin 1982), chitinozoans (Paris 1981) and conodonts (Sweet and Bergström 1984). All the regions belonging to it were located at high latitudes in the southern hemisphere; sedimentation during almost the entire Ordovician was of shallow-water clastics. This depositional pattern was interrupted only at the very end of the period by a single significant interval of carbonate deposition of variable but typically limited thickness regionally. The carbonates are primarily cystoid wackestones that are overlain by a thicker clastic sequence bearing glaciomarine diamictites associated with the Hirnantian (late Ashgill) glaciation (Robardet and Doré 1988; Robardet *et al.* 1990; Štorch 1990).

Knüpfner (1967) described the conodont fauna from this carbonate unit in Thuringia, but used only form taxonomy, typical of that time. This monographic work, together with the parallel study of the Tonflaserkalk from the Carnic Alps (Serpagli and Greco 1965; Serpagli 1967), initiated Mediterranean Province conodont investigations. Similar later studies include those of the Urbana Limestone of eastern and western Sierra Morena (Fuganti and Serpagli 1968; Hafenrichter 1979; Sarmiento 1990; Ferretti 1992), the Cystoid Limestone of the eastern Iberian Chain (Carls 1975; Hafenrichter 1979; Ferretti 1992), from Catalonia (Ferretti 1992), the Central Pyrenees in Spain (Hartevelt 1970), the Calcaire de Rosan of Brittany (Lindström and Pelhate 1971; Paris *et al.* 1982), the Calcaire de Vaux and calcareous boulders in the Tillite de Feuguerolles of Normandy (Weyant *et al.* 1977), Austrian Carnic Alps and Northern Greywacke Zone (Schönlaub 1969, 1979, 1980; Flajs and Schönlaub 1976), Sardinia (Helmcke and Koch 1974; Ferretti and Serpagli 1991), Libya (Bergström and Massa 1979, 1987, 1992) and Bohemia (Ferretti 1992).

An important synthesis of the upper Ordovician European conodont faunas and their biostratigraphy was given by Sweet and Bergström (1984), who reconstructed the main multielement taxa of the Thuringian fauna using published descriptions and illustrations. They revised Knüpfner's identifications at the multielement species level and new data were added later by Dzik (1989) and Fuchs (1989, 1990). Nevertheless, the precise age of the Kalkbank in Thuringia has never been



TEXT-FIG. 1. Geological map of Schmiedefeld area, Thuringia, after Knüpfner (1967), showing sample location.

established, as the M element of the *Amorphognathus* species, which is the critical one for species differentiation in this genus, was missing.

A sample which yielded over 25000 conodont elements, collected near Schmiedefeld (Text-fig. 1) and kindly provided by Wolfgang Hammann, forms the basis of this paper, in which the taxonomy of this new fauna and its biostratigraphical and palaeobiogeographical significance are assessed.

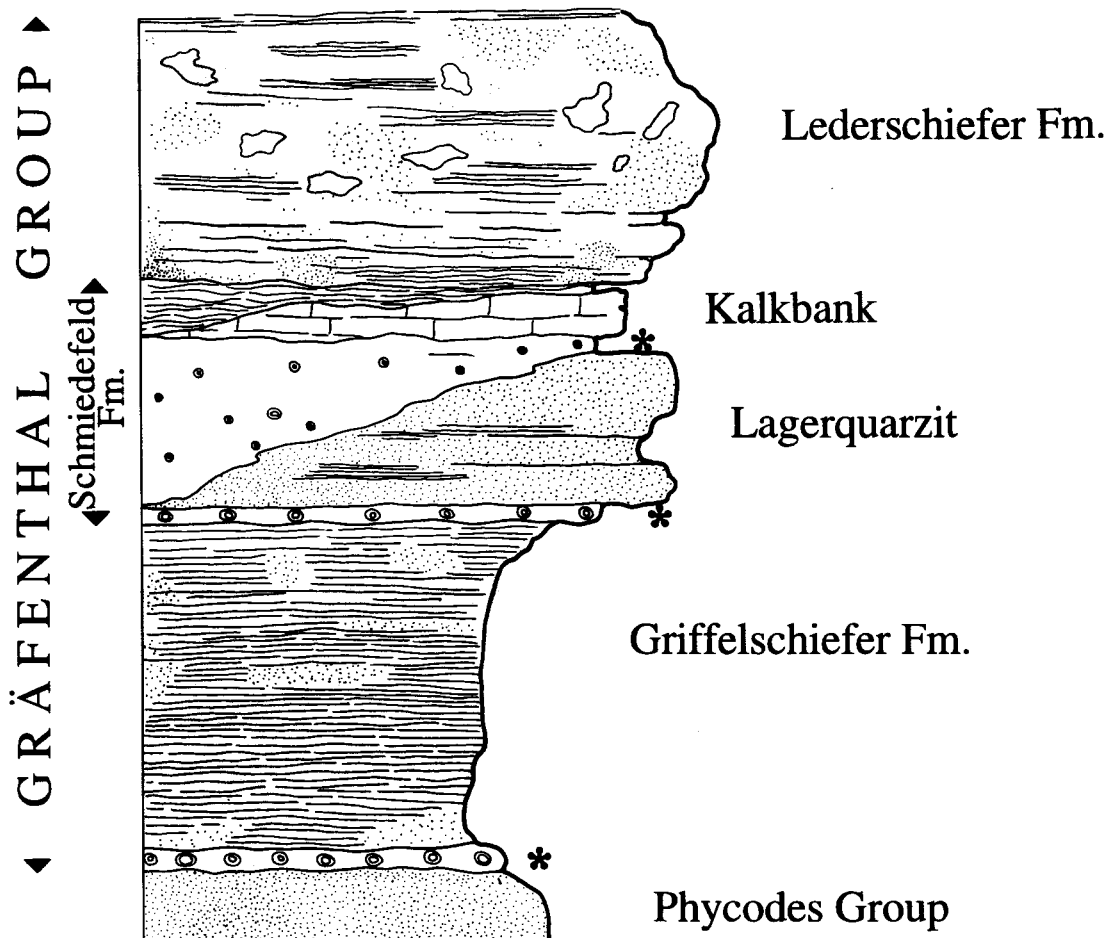
All the specimens described and figured are housed in the Micropalaeontological Collections of the Department of Earth Sciences of Modena University, Italy (repository numbers IPUM 24721-24866).

STRATIGRAPHICAL FRAMEWORK

Exposures near Wittmannsgereuth and Schmiedefeld (Text-fig. 1) have provided the best localities in Thuringia for the thin late Ordovician carbonate unit (Kalkbank). A chamosite-rich oolitic level, at the base of the limestone (Text-fig. 2) has supported several small iron mines, now mostly abandoned. In particular, the famous Gebersdorf mine was the source of most of Knüpfner's samples. Our material comes from near the slag heap of Gebersdorf mine, on the northern slope of the valley about 1 km north-east of Schmiedefeld (Text-fig. 1).

The Ordovician of Thuringia is represented by up to 3000 m of terrigenous clastics: in ascending order, on a Cambrian basement, the Frauenbach Group (up to 650 m), the Phycodes Group (up to 2000 m), and the relatively thin Gräfenenthal Group (about 400 m) which comprises the Griffelschiefer, Schmiedefeld and Lederschiefer formations (Text-fig. 2) of upper Arenig to uppermost Ordovician age.

At the base of the Griffelschiefer Formation (40–200 m), consisting of black shales, there is an iron-rich member, the 'Unterer Erzhorizont' (0–11 m). The Schmiedefeld Formation, which corresponds to the 'Oberer Erzhorizont' of Knüpfner (1967), is composed of two separate chamositic oolitic levels, the 'Unteres Erzlager' (0.2–8 m) and the 'Oberes Erzlager' (0–20 m), between which a quartzitic unit, the Lagerquarzit, of variable thickness (0–30 m), is usually intercalated. The top



TEXT-FIG. 2. Schematic stratigraphical section of the Gräfenenthal Group, after Knüpfner (1967), Steiner and Falk (1981) and Fuchs (1990). Note that the section is not to scale; the condensed section is expanded to show detailed stratigraphical relationships. Thickness of units is: up to 2000 m for the Phycodes Group, 40–200 m for the Griffelschiefer Formation, 0–30 m for the Lagerquarzit, 0.1–0.4 m for the Kalkbank and 40–250 m for the Lederschiefer Formation. Asterisks indicate iron-rich oolitic horizons.

of the formation is formed by the Kalkbank, a light grey, fine grained limestone usually 0.1–0.4 m thick (Knüpfner 1967), but which may locally be absent (Steiner and Falk 1981). From the Schmiedefeld Formation, conodonts, trilobites, brachiopods, ostracodes, foraminiferans, crinoids, bryozoans and gastropods have been reported (Knüpfner 1967). There is a discontinuity within the formation, between the Lagerquarzit and the 'Oberes Erzlager', whereas the other strata appear to have been deposited continuously (Knüpfner 1967; Fuchs 1990).

A thin slate (0.05–0.5 m) with dark flaser structures overlies the limestone (Steiner and Falk 1981) and is followed by the glaciomarine Lederschiefer Formation (40–250 m) containing supposedly ice transported, partly fossiliferous pebbles in the upper part. Rare bryozoans, crinoids, brachiopods and palynomorphs do not allow a precise biostratigraphical age assignment. Event stratigraphical considerations, however, suggest a correlation with similar diamictites of Hirnantian age widespread over the peri-Gondwana shelf. The basal beds of the overlying 'Untere Graptolithenschiefer' contain graptolites indicative of the Llandovery *Parakidograptus acuminatus* Biozone (Storch 1990).

TABLE 1. Number of individual conodont elements recovered from the Kalkbank limestone.

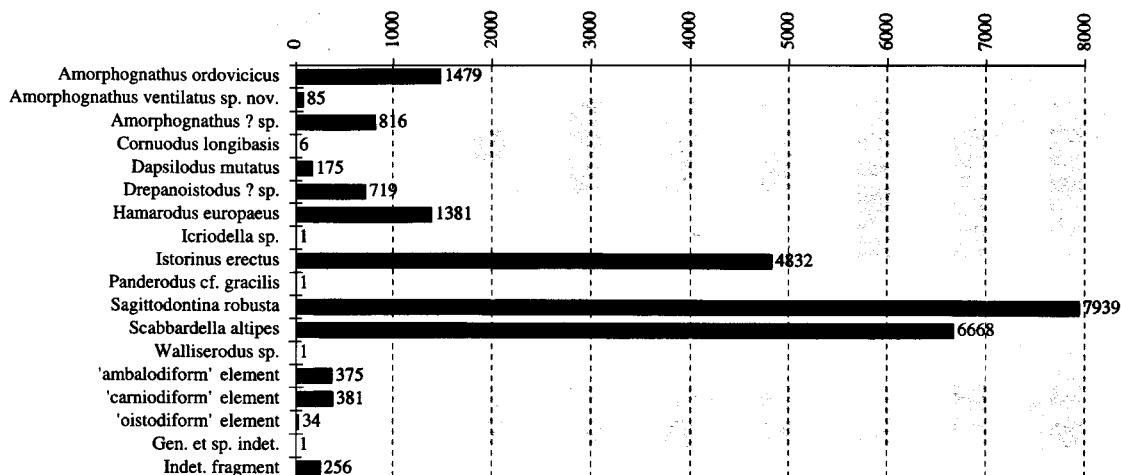
Species and elements	Number	Species and elements	Number
<i>Amorphognathus ordovicicus</i>		<i>Icriodella</i> sp.	1
Pa	356	<i>Istorinus erectus</i>	4832
Pb	321	<i>Panderodus</i> cf. <i>gracilis</i>	1
M	17	<i>Sagittodontina robusta</i>	
Sa	278	Pa	2749
Sb	221	Pb	246
Sc	198	M	459
Sd	88	Sa	1521
<i>Amorphognathus ventilatus</i> sp. nov.		Sb	1098
M	85	Sc	454
<i>Amorphognathus?</i> sp.	816	Sd	1412
<i>Cornuodus longibasis</i>	6	<i>Scabbardella altipes</i>	6668
<i>Dapsilodus mutatus</i>	175	<i>Walliserodus</i> sp.	1
<i>Drepanoistodus?</i> sp.	719	'ambalodiform' element	375
<i>Hamarodus europaeus</i>		'carniodiform' element	381
Pa	231	'oistodiform' element	34
Pb	91	Gen. et sp. indet.	1
M	468	Indet. fragment	256
Sa	79	Total	25 150
Sb	96		
Sc	397		
Sd	19		

THE KALKBANK CONODONT FAUNA

The 2.1 kg sample processed dissolved readily in a solution of 10 per cent. formic acid, and produced over 25000 conodont elements. Most have encrusted surfaces, many are fragmentary, and elements belonging to different species commonly have been found fused together. Nevertheless, they could be identified at the multielement species level, and many well preserved specimens also occur. The conodont Colour Alteration Index (CAI) (Epstein *et al.* 1977) of the specimens is 4, indicating burial temperatures in the range of 190–300 °C. The elements belonging to *Sagittodontina robusta* and *Istorinus erectus* appear slightly lighter in colour, but this is probably related to their limited wall thickness, and the cusp of some M elements and the apical part of some Pa and Pb elements of *Hamarodus europaeus* are sometimes paler than the rest of the specimen.

In this conodont fauna, 13 multielement species representing 11 genera have been identified, four of which are left in open nomenclature. The list and abundance of the species is given in Table 1 and Text-figure 3. The fauna is dominated by *Sagittodontina robusta* (32 per cent.), *Scabbardella altipes* (27 per cent.) and *Istorinus erectus* (19 per cent.); *Hamarodus europaeus* (5 per cent.) is also common. Other species, *Walliserodus* sp., *Panderodus* cf. *gracilis*, *Cornuodus longibasis* or *Icriodella* sp. are extremely rare. No stratigraphical or palaeoecological reasons appear to explain the paucity in this fauna of the cosmopolitan coniform genus *Panderodus*. A different hydrodynamic behaviour of these elements is a possible answer. Selective post-mortem transport could have occurred in which only a fraction of the original fauna was deposited in the Kalkbank unit, resulting in the dominance of apparently light elements such as those of *S. robusta*.

The relative proportion of species compares closely with that reported by Knüpfner (1967) (Text-fig. 3). However, a specific evaluation is difficult since the numerical data of Fuchs (1990) for *S. robusta* in Knüpfner's collection include elements of *I. erectus*, which we regard as a separate species. The great dominance of *S. altipes* reported by Fuchs in his collection is, as he also suggested,



TEXT-FIG. 3. Numbers of individual species recovered from the Kalkbank Limestone sample.

probably the result of the aggressive sample processing in the laboratory, that could have destroyed thin-walled elements with a deep basal cavity, such as those of *S. robusta*. In addition to the previously known fauna, species of *Icriodella* and *Cornuodus* are reported for the first time.

After comparison with collections of Ashgill conodonts from Whitland, South Wales, we doubt that '*Ambalodus triangularis triangularis* Branson and Mehl, 1993' from Knüpfers collection (1967, pl. 9, fig. 2a-b) and present in our fauna (Pl. 2, figs 11-13) could represent the Pb element of *Rhodesognathus* as previously supposed (Dzik 1989; Fuchs 1990). In fact the lateral process of the Pb elements of *Rhodesognathus* develops as an extension of the denticle anterior to the cusp, and not, as happens in our specimens, of the cusp itself. For the same reason, Bergström (1983, p. 46) regarded the '*Prioniodus*' (*Rhodesognathus*?) n. sp. aff. *Prioniodus variabilis* Bergström, 1962 and *Prioniodus gerdæ* Bergström, 1971 reported by Lindström *et al.* (1974) from Brittany as probable *Prioniodus* (*Baltoniodus*) rather than *Rhodesognathus*. Note that Dzik (1994) has recently underlined how the position of branching of the anterior process in the platform elements may be a useful character for distinguishing *Rhodesognathus*. After direct comparison with the material described from Spain by Carls (1975) and Hafenrichter (1979), their corresponding specimens of '*Ambalodus triangularis triangularis* Branson and Mehl, 1933' appear similar to ours. In addition, the elements classified as '*Ambalodus robustus* Rhodes, 1953' by Knüpfers (1967, pl. 10, figs 7-8) are more likely, in our opinion, to be anterior processes of an 'amorphognathiform' platform that we have left in open nomenclature (Pl. 2, figs 1-4), and not the Pa elements of *Rhodesognathus* (Dzik 1989; Fuchs 1990). The specimens of *Rhodesognathus elegans* reported by Lindström and Pelhate (1971) from the Calcaire de Rosan in Brittany and by Sarmiento (1990) from the Urbana Limestone of eastern Sierra Morena were neither figured nor described, and so it is impossible to attempt any comparison, but, to date, represent the only reports of this species in the Mediterranean Province. New investigations will probably reveal whether this form can be regarded as a palaeogeographical marker for lower latitudes and of warmer water compared with the cool water environment inferred for the Kalkbank.

THE AGE OF THE KALKBANK LIMESTONE

Knüpfers (1967) described his fauna using form element taxonomy; 58 species belonging to 26 genera were recognized, including the important new genera *Sagittodontina* and *Istorinus*. On the basis of conodont and trilobite faunas, Knüpfers suggested that the age of the limestone was close to the Caradoc-Ashgill boundary.

Subsequently, in a general study of *Amorphognathus*, Lindström (1977) referred the morpho-species figured by Knüpfer to *A. ordovicicus*. Sweet and Bergström (1984) reinterpreted the Thuringian fauna and recognized nine multielement species including *A. cf. ordovicicus*. The identifications in both these studies were based mainly on the platform elements figured by Knüpfer, as no unequivocal M elements were recognized.

In a different approach, Dzik (1989) recognized *A. superbus*, based on the assumption that the single specimen of 'Holodontus sp.' in Knüpfer's collection (pp. 30–31, pl. 3, fig. 14) was the M element of the species. In addition, he also observed that Pa elements of *A. superbus* are generally larger than the corresponding ones of *A. ordovicicus*. Fuchs (1990), by the use of acetic and phosphoric acid, recovered about 250 additional elements, but no M elements. Nevertheless, he assigned the Kalkbank to the *A. superbus* Zone (Caradoc to lower Ashgill), basing his identification on the specimen of 'Holodontus sp.' mentioned above.

The presence of many M elements in our fauna represents an important discovery. Seventeen of *A. ordovicicus* have been found together with 85 of *A. ventilatus* sp. nov., and are described below. The latter lack the anterior aboral denticle that is typical of 'Holodontus superbus Rhodes, 1953', the M element of *Amorphognathus superbus*. However, they do possess a very long anterior aboral process and the cusp is not discrete as in 'Goniodontus superbus Ethington, 1959', the corresponding M element of *A. ordovicicus*. On the outer lateral edge of the cusp, and not on the outer lateral process, they generally have two or three small denticles growing at a different angle towards the axis of the cusp. All these features are more typical of the M element in *A. superbus*, although some features of the *A. ordovicicus* M element are definitely present. It is difficult to judge from a single sample, even with an abundant fauna, whether this new species represents a transitional evolutionary stage. A similar form was figured by Viira (1974, p. 90, fig. 110) from the Ohesaare core from Estonia, but unfortunately no other elements of that fauna indicate taxonomic or stratigraphical relationship. The horizon from which her element was recovered is immediately below an *ordovicicus* fauna (Lindström 1977), while a *superbus* fauna occurs in the lowermost part of the core interval referred to the Nabala Stage (Bergström 1971). Lindström (1977) regarded this element, with question, as the M element of *A. complicatus*, but in the Kalkbank material no platform elements of this latter species occur to verify this possibility.

The different elements found could presumably represent a reworked assemblage. However, there are no significant differences in preservation that are typical for reworked conodonts. This potential explanation is rejected. Nevertheless, the evolution of the M element in the *Amorphognathus* lineage, starting from the older *A. tvaerensis*, shows a gradual reduction in number, and final disappearance of the denticles on the inner anterior process, a contraction of the anterior aboral process which eventually disappears in *A. ordovicicus*, the development of a prominent and discrete cusp, a reduction of its inclination, and an increase in cusp size. It is noteworthy that Orchard (1980) reported some M elements, lacking accessory denticles on the cusp but with three well-developed processes, as *A. aff. superbus*, from the upper part of the *superbus* zone from the Crûg and Birdshill limestones in South Wales.

In summary, we consider the age of the Kalkbank limestone to be early Ashgill, equivalent to the base of the *ordovicicus* Zone. The similar limestones that were deposited in other parts of the Mediterranean Province appear to be slightly younger, but within this zone (Ferretti 1992). This difference may be in response to ecological and/or oceanographical events that initiated calcareous sedimentation diachronously in the diverse areas. Finally, only the discovery of additional abundant samples, perhaps in other areas of Thuringia, and new data will reveal whether the Kalkbank represents a condensed unit equivalent to entire sequences deposited during the Ashgill elsewhere in southern Europe, or only to their older part.

TAXONOMIC REMARKS: THE *AMORPHOGNATHUS* LINEAGE

Although the Kalkbank fauna was recovered from a single sample and the faunal composition is similar in general to earlier reports (Knüpfer 1967; Dzik 1989; Fuchs 1989, 1990), it is its sheer

abundance that is remarkable, and which allows a more complete taxonomic description of the dominant species. In particular, there is a substantial number of specimens of three forms of *Amorphognathus* (*A. ordovicicus*, *A. ventilatus* sp. nov., *A.?* sp.). This study, together with one nearing completion on coeval basal Ashgill faunas from Whitland, South Wales raises doubts concerning the rather simple pattern of evolution in the *Amorphognathus* lineage previously proposed (e.g. Bergström 1971, 1983; Sweet and Bergström 1976; Dzik 1989, 1994), i.e. from *A. tvaerensis* through *A. superbus* to *A. ordovicicus* on which the upper Ordovician conodont biozonation is based. The relationship of other late Ordovician species of *Amorphognathus* (e.g. *A. complicatus*, *A. lindstroemi*) to this main lineage has not been established; these two species are less widely distributed and perhaps overlooked.

As noted above and described below, the M element of *A. ventilatus* sp. nov. bears some peculiar morphological characteristics that suggest that it may have evolved from *A. superbus*. In addition to the *tvaerensis*–*superbus*–*ordovicicus* lineage there may be at least one other in the late Ordovician, culminating in *A. lindstroemi*. As partly reflected in our synonymies for *Amorphognathus* species, we suspect that the complexity of evolution within *Amorphognathus* has been masked by some earlier workers assigning different forms into one or more of the three species in the main lineage. With new studies under way it may be possible to refine further the upper Ordovician conodont biozonation through an improved understanding of phylogenetic relationships within *Amorphognathus*.

Aldridge *et al.* (1995) established the apparatus architecture of *Promissum pulchrum* Kovács-Endrödy based on over 100 complete apparatuses preserved on bedding planes of the upper Ordovician Soom Shale Member, Cedarberg Formation, South Africa. *Promissum*, like *Amorphognathus*, has a prioniodontid apparatus plan, but includes not only Pa and Pb elements, but also Pc and Pd elements. Aldridge *et al.* (1995) considered that other Ordovician prioniodontid taxa may also include Pc and/or Pd elements (e.g. *Gamachignathus*). From the Kalkbank material, we have yet to recognize elements in *Amorphognathus* that could be assigned unequivocally as Pc or Pd elements.

PALAEOGEOGRAPHICAL REMARKS

Conodonts belonging to the Mediterranean Province have a special value, as they represent a high latitude fauna living in polar to subpolar environments (Sweet and Bergström 1984; Bergström and Massa 1992). Some of them are typical of this region, and are absent from coeval faunas of inferred lower and middle latitudes. *Sagittodontina robusta* and *Istorinus erectus* are probably the best indicators of the Mediterranean Province. So far, both of these species seem to be most abundant in Thuringia, but this may reflect a slight age difference and/or ecological factors. This Kalkbank fauna reinforces the strong faunal similarity noted above between Thuringia, Libya, Spain and France. Elements of *S. cf. robusta* have been found also in the Perník Bed of Bohemia (Ferretti 1992), but the fauna is poor and too sparse to allow more specific conclusions. The two indicator species have so far not been found in Sardinia and the Carnic Alps. This latter region appears to have the most diversified fauna in southern Europe and to have had closer relations to more temperate faunas, such as those in Britain, having several taxa in common that have not been reported elsewhere in southern Europe. Bohemia (Marek and Havlíček 1967; Havlíček 1976, 1977), Sardinia (Leone *et al.* 1991) and the Carnic Alps (Schönlaub 1971; Jaeger *et al.* 1975) are so far the only regions in southern Europe from which a shelly Hirnantian fauna has been reported. This probably reflects different latitudinal/ecological conditions. Finally, *Rhodesognathus elegans* could prove to be a valuable index species of more temperate regions.

From South Africa, another area of Gondwanaland within high latitudes in the late Ordovician, a new conodont fauna has been described (Theron *et al.* 1990; Aldridge *et al.* 1994; Aldridge *et al.* 1995). Over 100 bedding plane assemblages of *Promissum pulchrum* have been found, some preserving soft tissue impressions. The elements are up to an order of magnitude larger than most late Ordovician conodonts. The palaeobiogeographical and palaeoecological significance of this fauna is not yet clear. The monospecific fauna occurs in a subpolar, non-carbonate facies and has

not been found elsewhere. It could represent an even colder water fauna than that of the Mediterranean Province.

Only recently has more attention been directed towards the thin iron-rich oolitic horizons below the limestones that are a feature typical of the different sequences in south-west Europe and adjacent areas, including the Ossa Morena Zone, Celtiberia, Normandy, Brittany, Libya, Thuringia and Bohemia (Young 1992, fig. 1). Young (1989) recognized these horizons at three stratigraphical intervals in the Ordovician: lower Llanvirn, the lower Caradoc and the lower Ashgill. They represent 'sediments formed under extremely low sedimentation rates and were most commonly developed as the initial deposit above a disconformity ... [they] form important marker horizons for correlation within the region' (Young 1992, p. 321). We consider it probable, therefore, that iron-rich oolitic levels were deposited in the early Ashgill almost simultaneously over most of the Gondwana shelf and initiated a new depositional sequence with basal terrigenous deposits, overlain by younger limestones in some shallower and/or higher latitude areas (i.e. Celtiberia or Ossa Morena) and already calcareous in other apparently more offshore and/or lower latitude and possibly condensed sequences, as in Thuringia.

SYSTEMATIC PALAEOLOGY

Orders and families are mostly from Sweet (1988). Synonymy lists are limited to references to the first description of morphospecies, first apparatus reconstruction and recent reports. Descriptions are given only if new information is provided by the fauna examined. Diagnoses are limited to new species. For complete data, see Dzik (1994).

Order BELODELLIDA Sweet, 1988?

Family ANSELLIDAE Fähræus and Hunter, 1985?

Genus HAMARODUS Viira, 1974

Type species. Distomodus europaeus Serpagli, 1967.

Hamarodus europaeus (Serpagli, 1967)

Plate 3, figures 1–14

- 1955 *Microcoelodus?* sp. Rhodes, p. 133, pl. 10, figs 15, 19, 22.
 1955 *Cordylodus elongatus* Rhodes; Rhodes, p. 135, pl. 7, figs 5–6.
 1959 *Oistodus* n. sp. Lindström, p. 440, pl. 3, fig. 13.
 1959 *Cordylodus* n. sp. Lindström, p. 438, pl. 3, figs 34–36.
 1964 ?*Neoprioniodus brevirameus* Walliser, p. 47, pl. 4, fig. 5; pl. 29, figs 5–10.
 1964 ?*Roundya prima* Walliser, p. 71, pl. 4, fig. 6; pl. 31, figs 1–2.
 1966 *Oistodus brevis* Branson and Mehl; Hamar, p. 63, pl. 1, fig. 19; text-fig. 4 (11).
 1966 N. genus and n. sp. Hamar, p. 77, pl. 3, figs 8–10; text-fig. 5 (5a–b).
 1967 *Distomodus europaeus* Serpagli, p. 64, pl. 14, figs 1–6.
 1967 'Oistodus' *niger* Serpagli, p. 79, pl. 20, figs 1–7.
 1967 *Oistodus abundans* Branson and Mehl; Knüpfer, p. 34, pl. 5, fig. 4.
 1976 *Hamarodus europaeus* (Serpagli); Dzik, p. 435, text-fig. 36.
 1980 *Hamarodus europaeus* (Serpagli); Orchard, p. 21, pl. 4, figs 22, 25, 29–31.
 1985 *Hamarodus europaeus* (Serpagli); Bergström and Orchard, pl. 2.5, figs 4, 7, 12.
 1989 *Hamarodus europaeus* (Serpagli); Dzik, text-fig. 16.
 1991 *Hamarodus europaeus* (Serpagli); Ferretti and Serpagli, pl. 2, figs 1–6.
 1994 *Hamarodus brevirameus* (Walliser); Dzik, p. 111, pl. 24, figs 14–19; text-fig. 31a.

Remarks. *Hamarodus europaeus* is common in our fauna, in which all the morphotypes are present. Surprisingly, Knüpfer's (1967) collection lacks Pa and Pb elements, which are the most typical representatives of the species. In our material, they are laterally compressed with a deep, wide basal

cavity and sharp anterior, upper and posterior margins. The wall is rather thin in most specimens, and, as a consequence, appears lighter in colour. The apical part of the cusp is commonly paler. The terminal denticulation of the anterior and upper keels is commonly broken. Pa elements are more abundant than Pb elements.

The M element is the most common component of the apparatus. It displays high variability in the angle between the posterior and upper margin and in the profile of the anterior margin, which may be variably curved. Lateral faces have no costae or other ornamentation. Only the larger elements appear completely black, while the smaller ones have a paler colour. The ratio of P to M elements in our fauna is 0.69, closer to that in Serpagli's (1967) material from the Carnic Alps (0.46) than to that in Orchard's (1980) collection from Great Britain (0.29).

The posterior process of S elements, extending at about 90° from the cusp, has a hindeodellid denticulation pattern. Fragments of these bars were probably regarded by earlier authors as 'carniodiform' elements. Distinction between the Sb and Sd elements is difficult, due in part to the poor preservation of our material. As the anterior denticles are not always recognizable, the presence of the lateral ones has been considered diagnostic. We follow Sweet (1988) in placing *Hamarodus* questionably in the family Ansellidae.

Occurrence. Upper middle and upper Ordovician of Europe (Thuringia, Carnic Alps, Spain, ?France, Great Britain, Estonia, Norway, Sardinia, Sweden, Bohemia, Poland) and China.

Family BELODELLIDAE Khodalevich and Tschernich, 1973

Genus WALLISERODUS Serpagli, 1967

Type species. *Acodus curvatus* Branson and Branson, 1947.

Walliserodus sp.

Plate 1, figure 24

Description. Only one fragment, lacking the basal area, is present. Two prominent costae are developed on the lateral faces of the element but they fade apically. Cross section outline slightly biconvex.

Occurrence. *Walliserodus* is known from the upper Ordovician and Silurian of Europe, North America, Australia and Asia.

Family DAPSILODONTIDAE Sweet, 1988

Genus DAPSILODUS Cooper, 1976

Type species. *Distacodus obliquicostatus* Branson and Mehl, 1933.

Dapsilodus mutatus (Branson and Mehl, 1933)

Plate 3, figures 15–19

- 1933 *Belodus? mutatus* Branson and Mehl, p. 126, pl. 10, fig. 17.
- 1959 *Acodus inornatus* Ethington, p. 268, pl. 39, fig. 11.
- 1959 *Distacodus procerus* Ethington, p. 275, pl. 39, fig. 8.
- 1967 *Acodus curvatus* Branson and Branson; Serpagli, p. 41, pl. 6, fig. 3a–c.
- 1967 *Acodus mutatus* (Branson and Mehl); Serpagli, p. 41, pl. 6, figs 1a–b, 6a–b.
- 1967 *Acontiodus procerus* (Ethington); Serpagli, p. 46, pl. 9, figs 6–11.
- 1980 *Dapsilodus mutatus* (Branson and Mehl); Orchard, p. 20, pl. 5, figs 6, 15–16, 21.
- 1994 *Dapsilodus mutatus* (Branson and Mehl); Dzik, p. 64, pl. 11, figs 24–26, 31–35; pl. 14, figs 8–9; text-fig. 6d.

Remarks. Representatives of *Dapsilodus mutatus* are relatively common in our collection. Little can be added to the detailed observations already given by earlier authors on the single morphotypes. In addition, the poor preservation prevents the recognition of the antero-aboral costae on the lateral faces described in the Keisley Limestone specimens by Orchard (1980) or the striations figured in the Swedish specimens by Löfgren (1978). The morphospecies '*Oistodus venustus* Stauffer, 1935' is absent in our fauna; another type of 'oistodiform' element of uncertain taxonomic status has been left in open nomenclature.

Occurrence. Middle and upper Ordovician of Europe (Great Britain, Thuringia, Sardinia, Carnic Alps, Spain, Bohemia, Norway, Sweden, Estonia, Poland), North America, China and Libya.

Order PANDERODONTIDA Sweet, 1988
Family PANDERODONTIDAE Lindström, 1970
Genus PANDERODUS Ethington, 1959

Type species. *Paltodus unicastatus* Branson and Mehl, 1933.

Panderodus cf. gracilis (Branson and Mehl, 1933)

Plate 1, figure 23

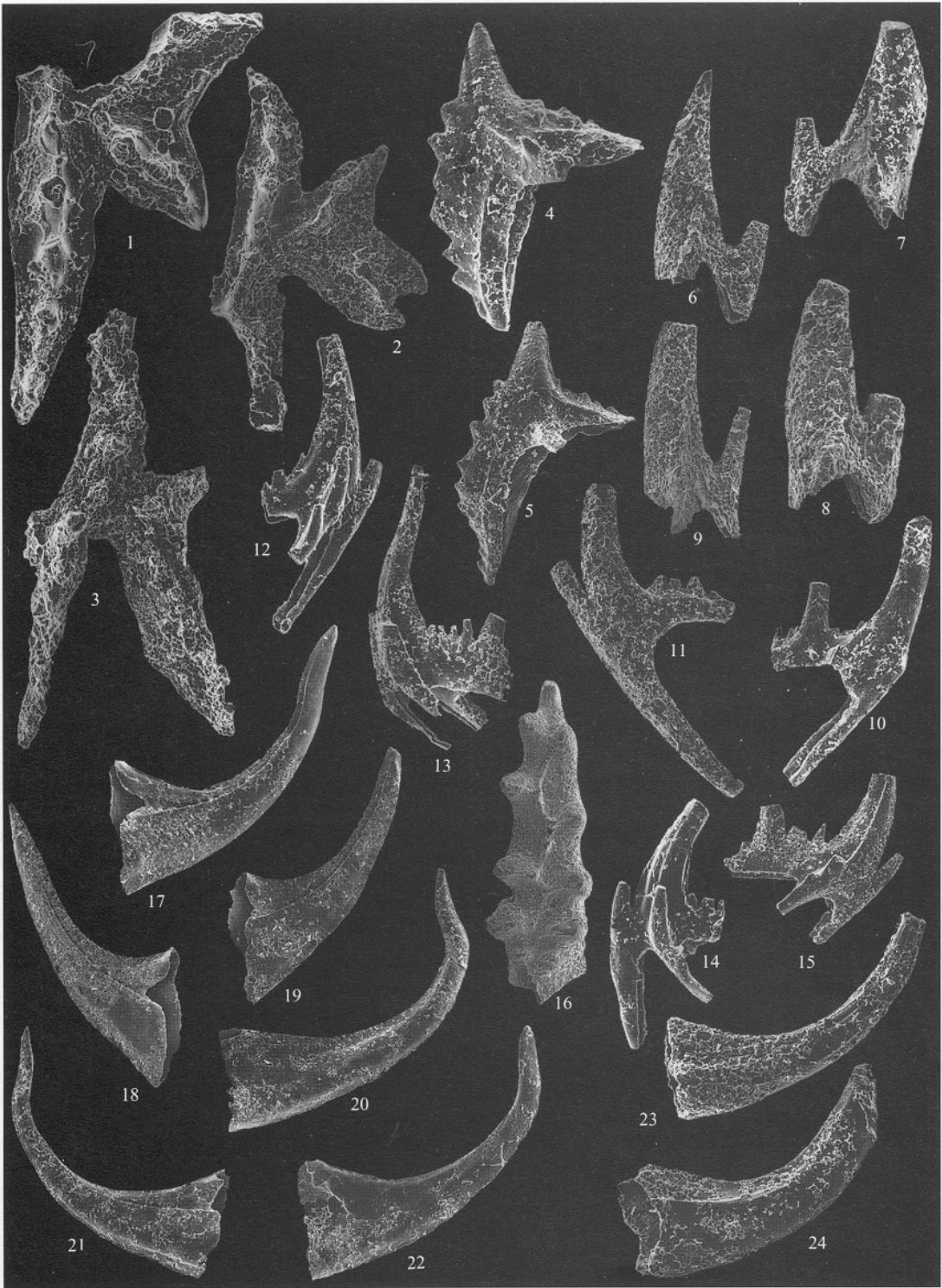
- cf. 1933 *Paltodus gracilis* Branson and Mehl, p. 108, pl. 8, figs 20–21.
cf. 1967 *Panderodus gracilis* (Branson and Mehl); Serpagli, p. 85, pl. 23, figs 3–5.
cf. 1976 *Panderodus gracilis* (Branson and Mehl); Dzik, p. 428, fig. 15a–b, e–f.

Remarks. Only one small but complete specimen is present in our collection. A principal costa is developed on each lateral face of the element; minor longitudinal striations run close to the upper margin. The single specimen does not allow an assignment within the new apparatus architecture model which was proposed recently for *Panderodus* by Sansom *et al.* (1995).

Occurrence. *P. gracilis* is well represented in the Ashgill of Europe, North America and Asia and ranges from the middle Ordovician into the Silurian.

EXPLANATION OF PLATE 1

- Figs 1–15. *Amorphognathus ordovicicus* Branson and Mehl, 1933. 1–3, IPUM 24721, IPUM 24722, IPUM 24723; upper views of Pa elements; $\times 130$, $\times 95$ and $\times 95$. 4–5, IPUM 24724, IPUM 24725; antero-lateral views of sinistral Pb elements; $\times 130$ and $\times 95$. 6–9, IPUM 24726, IPUM 24727, IPUM 24728, IPUM 24729; postero-lateral views of M elements; $\times 110$, $\times 130$, $\times 110$, $\times 100$. 10–11, IPUM 24730, IPUM 24731; antero-lateral views of Sc elements; $\times 120$, $\times 105$. 12, IPUM 24732; lateral view of Sa element; $\times 120$. 13, IPUM 24733; lateral view of Sd element; $\times 120$. 14–15, IPUM 24734, IPUM 24735; lateral views of Sb elements; $\times 125$, $\times 110$.
- Fig. 16. *Icriodella* sp.; IPUM 24736; upper view of anterior process of Pa element; $\times 50$.
- Figs 17–22. *Scabbardella altipes* (Henningsmoen, 1948). 17, IPUM 24737; $\times 60$; 18, IPUM 24738; $\times 60$; 19, IPUM 24739; $\times 60$; 20, IPUM 24740; $\times 45$; 21, IPUM 24741; $\times 60$; 22, IPUM 24742; $\times 45$. All lateral views.
- Fig. 23. *Panderodus cf. gracilis* (Branson and Mehl, 1933); IPUM 24743; lateral view; $\times 100$.
- Fig. 24. *Walliserodus* sp.; IPUM 24744; lateral view; $\times 95$.



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Order PRIONIODONTIDA Dzik, 1976

Family BALOGNATHIDAE Hass, 1959

Genus AMORPHOGNATHUS Branson and Mehl, 1933

Type species. Amorphognathus ordovicica Branson and Mehl, 1933.

Amorphognathus ordovicicus Branson and Mehl, 1933

Plate 1, figures 1–15

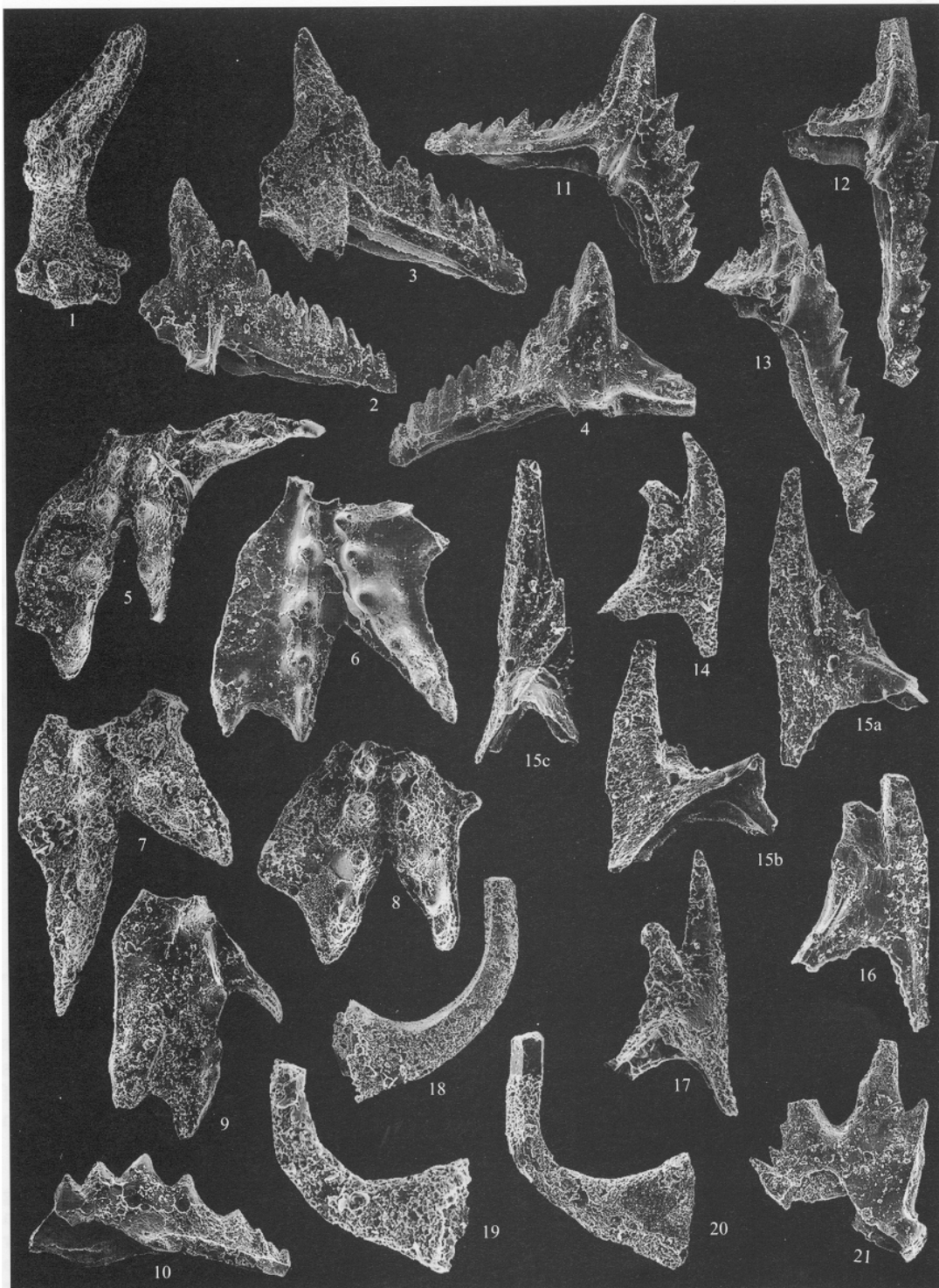
- 1933 *Amorphognathus ordovicica* Branson and Mehl, p. 127, pl. 10, fig. 38.
 1933 *Ambalodus triangularis* Branson and Mehl, p. 128, pl. 10, figs 35–37.
 1955 *Roundya diminuta* Rhodes, p. 137, pl. 8, figs 9, 12; pl. 9, fig. 6.
 1955 *Keislognathus gracilis* Rhodes, p. 131, pl. 7, figs 7–8; pl. 8, figs 10, 13–16.
 1955 *Ligonodina* cf. *L. elongata* Rhodes; Rhodes, p. 134, pl. 8, figs 7–8.
 1955 *Rosagnathus superbus* Rhodes, p. 129, pl. 7, figs 1–4.
 1959 *Goniodontus superbus* Ethington, p. 278, pl. 40, figs 1–2.
 1971 *Amorphognathus ordovicicus* Branson and Mehl; Bergström, p. 134, pl. 2, figs 6–7.
 1978 *Amorphognathus ordovicicus* Branson and Mehl; Bergström, pl. 80, figs 1–11.
 1980 *Amorphognathus ordovicicus* Branson and Mehl; Orchard, p. 16, pl. 4, figs 1–13, 17–18.
 1983 *Amorphognathus ordovicicus* Branson and Mehl; Nowlan, p. 660, pl. 2, figs 16–17, 22, 25–27.
 1986 *Amorphognathus ordovicicus* Branson and Mehl; Savage and Bassett, p. 691, pl. 84, figs 1–21; pl. 85, figs 1–26; pl. 86, figs 1–13.
 1991 *Amorphognathus ordovicicus* Branson and Mehl; Ferretti and Serpagli, pl. 1, figs 1–9.
 1992 *Amorphognathus* sp. cf. *A. ordovicicus* Branson and Mehl; Bergström and Massa, p. 1337, pl. 1, figs 18–24.
 ?1994 *Amorphognathus ordovicicus* Branson and Mehl; Dzik, p. 94, pl. 23, figs 6–12; ?pl. 24, fig. 20; text-figs 21c, 22.

Remarks. No intact Pa elements are present in our fauna, and only a few are complete enough to allow a specific identification. Nevertheless, both sinistral and dextral forms have been found, and the blade type and non blade type of anterior process described by Bergström (1964) are present. Only isolated or coupled processes have been counted in the attempt to give a more realistic numerical estimation of the fauna.

Pb elements display high variability, both in sinistral and dextral form, involving the general size, the angle between the anterior and posterior processes and the upper profile of the anterior process. Some larger specimens have the anterior and posterior processes more aligned; in some smaller elements the upper margin of the anterior process appears more recurved in outer lateral view. The distinction between these two types is not always clear, as many transitional forms are present.

EXPLANATION OF PLATE 2

- Figs 1–10. *Amorphognathus?* sp. 1–4, upper view and lateral views of IPUM 24745; × 100; IPUM 2746; × 100; IPUM 24747; × 90; IPUM 24748; × 95. 5–9, upper views of IPUM 24749; × 100; IPUM 24750; × 90; IPUM 24751; × 90; IPUM 24752; × 125; IPUM 24753; × 95. 10, IPUM 24754; lateral view; × 75.
 Figs 11–13. ‘ambalodiform’ elements. 11, IPUM 24755; × 90. 12, IPUM 24756; × 95. 13, IPUM 24757; × 90. All lateral views.
 Figs 14–17. *Amorphognathus ventilatus* sp. nov. 14, IPUM 24758; antero-lateral view; × 120. 15a–c, holotype, IPUM 24759; antero-lateral, oral and postero-lateral views; × 150, × 170, × 165. 16, IPUM 24760; antero-lateral view; × 150. 17, IPUM 24761; lateral view; × 135.
 Figs 18–20. *Cornuodus longibasis* (Lindström, 1955). 18, IPUM 24762; × 90. 19, IPUM 24763; × 130. 20, IPUM 24764; × 95. All lateral views.
 Fig. 21. Gen. et sp. indet.; IPUM 24765; lateral view; × 95.



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Savage and Bassett (1986) regarded the variability of the Pb element as a possible key to identification of *Amorphognathus* species, being smaller and more robust in *A. ordovicicus* compared with the corresponding elements of older species. Recently, Bergström and Massa (1992) rejected this interpretation, as the Pb element appeared too similar in the different species of the genus to be diagnostic. It is impossible to establish if the variability observed in our specimens represents different species or simply intraspecific variation.

In describing the apparatus of *Promissum pulchrum* from the upper Ordovician of South Africa, Aldridge *et al.* (1995) established the presence of Pc and Pd elements in addition to Pa and Pb elements within the prioniodontid apparatus plan. They suggested that other Ordovician prioniodontid genera (e.g. *Gamachignathus*) and certainly some Silurian (e.g. *Pterospathodus*, *Coryssognathus*, *Astropentagnathus*) may also possess Pc and/or Pd elements. Despite the high number of platform elements, we are unable to recognize unequivocally Pc or Pd elements within the apparatus of *Amorphognathus* as represented in the Kalkbank collection.

M elements show the typical features described by Ethington (1959) and subsequently redefined by Serpagli (1967). The anterior inner lateral process is reduced in all our specimens. The anterior outer lateral process, if not broken, is always denticulated, carrying a main denticle and some minor ones distally, located in the space between the cusp and the main outer denticle or on the outer process. In one specimen (Pl. 1, fig. 7) a small denticle was observed close to the main lateral denticle. The posterior process can be adenticulated, even if long, or may carry a single small denticle.

S elements are present in different proportions, being the Sa, Sb and Sc in similar proportions, while the Sd elements are rare.

The approximate ratio of Pa, Pb, M and S elements is respectively 21:19:1:46. This value is only approximate as we have preferred to keep separate some fragments of a possible Pa element of *Amorphognathus?* sp. and some M elements of *A. ventilatus* sp. nov., that could have shared many of the elements here included in *A. ordovicicus*.

Occurrence. *Amorphognathus ordovicicus* is well known in the upper Ordovician of Europe, North America and part of Asia. It is known in Europe from Spain, north-west France, the Carnic Alps and adjacent areas of Austria, Sardinia, Thuringia, Bohemia, Poland, Sweden, Estonia and the British Isles.

Amorphognathus ventilatus sp. nov.

Plate 2, figures 14–17

1974 *Holodontus* n. sp. Viira, p. 90, fig. 110 (only).

Derivation of name. From the Latin *ventilare* (= to fan).

Holotype. M element IPUM 24759; Pl. 2, fig. 15a–c; Kalkbank limestone, Gebersdorf mine, Schmiedefeld, Thuringia, Germany.

Diagnosis. Compound M ('holodontiform') element consisting of a cusp from which three processes develop. General profile that of a deformed pyramid, with unequal triangular faces, each process representing an edge. Inner anterior process is thin, long and has no denticles. On outer edge of cusp, at mid-height, generally two or three sharp denticles are developed with a divergent direction of growth to axis of cusp. Denticles commonly fused together in a kind of fan.

Description. Both sinistral and dextral forms are present. The oral margin appears quite asymmetrical, being completely straight on the inner side, and denticulated on the outer. Lateral denticles are generally smaller than the cusp, which has a prominent position on element. The posterior process is directly connected to the anterior outer process with a ridge, giving a typical triangular profile in outer-lateral view. The anterior face of the cusp is planar to slightly convex; the posterior face is convex. The cusp is slightly flexed postero-laterally. The posterior process is non-denticulated. In some specimens the oral edge of the posterior process extends to the

outer edge of fan, and not along the cusp. The large basal cavity is triangular in aboral view and extends beneath the processes as a groove.

Remarks. Only the M element of *A. ventilatus* sp. nov. has been clearly recognized. Other elements of the apparatus are probably conflated with those of *A. ordovicicus* and possibly, with *Amorphognathus?* sp.

A specimen similar to our M elements was described and figured by Viira (1974, p. 90, fig. 110) as '*Holodontus* n. sp.' from the Ohesaare core in Estonia (depth 461.95 m). Three elements from the overlying formation (Viira 1974, pl. 13, figs 29–31) were included in the same morphospecies, but probably belong to *A. ordovicicus* (see Lindström 1977). Viira's (1974, fig. 110) '*Holodontus* n. sp.' appears to have a small denticle on the inner lateral process, a feature not observed in our specimens. Lindström (1977) included this element questionably in *Amorphognathus complicatus*. Unfortunately, we have few platform elements complete enough to allow specific identification, but none belongs to that species. Some of the 'ambalodiform' elements of our fauna resemble '*Ambalodus frognoeyensis* Hamar, 1966', the Pb element of *A. complicatus*, but we do not regard it as diagnostic.

The single specimen of '*Holodontus* sp.' described by Knüpfer (1967) undoubtedly shows, according to his description and illustration, many similarities to the M element of *A. ventilatus* sp. nov., but it appears to lack a real cusp. Two M elements of *A. superbus* described by Savage and Bassett (1986, pl. 83, figs 13–14) seem to develop two denticles only on one edge of a main denticle, which is not sufficiently prominent to be considered a real cusp.

The characteristic disposition of the denticles in a kind of fan on the outer side of the cusp seems typical of the species and has not been recorded in other 'holodontiform' elements. In addition, the M element of *A. ventilatus* sp. nov. differs from '*H. superbus* Rhodes, 1953' in the absence of the anterior aboral denticle, and from '*Goniodontus superbus* Ethington, 1959' in retaining a well-developed anterior process. A similarity, especially in outer-lateral view, occurs in some specimens of '*G. lindstroemi* Serpagli, 1967' (pl. 16, figs 2–4), but the latter lack a long anterior inner process and the ray of denticles on the outer edge of the cusp. The possible phylogenetic relationships of this element to other species of *Amorphognathus* are discussed above.

Occurrence. Upper Ordovician of Thuringia and Estonia.

Amorphognathus? sp.

Plate 2, figures 1–10

- 1967 *Ambalodus robustus* Rhodes; Knüpfer, p. 20, pl. 10, figs 7–8, ?9.
1990 *Rhodesognathus elegans* (Rhodes); Fuchs, p. 206, pl. 6, fig. 3.

Description. Several Pa fragments present in our fauna are described separately because of: their larger size compared with platform elements of *A. ordovicicus*; the special denticulation of platform; the dark colour; and presence of a prominent cusp on the anterior process. Two variants are recognized.

One type (Knüpfer 1967, p. 20, pl. 10, figs 7–8) is represented by narrow blade-shaped processes (Pl. 2, figs 1–4). In oral view, they are straight or slightly sinuous, with submedian crest with rather high and narrow denticles that generally increase in size towards the cusp. Only one of them, although badly preserved, was complete enough to show, posterior to the cusp, the beginning of a platform bearing two parallel denticles with thin costa developing at 90° from one of them (Pl. 2, fig. 1). A well-developed ledge runs along the basal margin and continues along the lateral process. On one side of the cusp, a shallow, narrow groove continues directly into what was probably the lateral process, but this is never preserved completely in our specimens. The cusp may be erect or slightly recurved posteriorly and has rounded edges. Between the cusp and platform is an area that is undenticulated or which bears one or two small denticles. The outer margin is generally straight, and then opens on a platform. In lateral view of very sinuous forms, the outer basal edge of process may be visible. The basal cavity is narrow and deep.

A second type (Knüpfer 1967, ?pl. 10, fig. 9) is represented by wider fragments, commonly arched, that may be non-blade anterior processes (Pl. 2, fig. 10). The longitudinal median crest is composed of smaller, wider and equidimensional denticles. The basal ledge is commonly missing.

Platforms that could have been attached to these processes are never complete, and have a lighter colour. The best preserved (Pl. 2, figs 5–9) are composed of both main (posterior) process, probably growing along the same line of cusp, and another bilobate (inner) process. A darker edge is present almost all around the platform. The posterior process has a variable length: it can be of the same size as the posterior-inner one or longer. The anterior-inner bar is at almost 90° from the posterior-inner one. Denticles are nodose and disposed slightly towards the inner side of the process, and are not exactly central. Those of the posterior-inner process run almost parallel to those of the posterior process. The anterior-inner process has maximum of three denticles developed along a line that merges with the first denticle of the posterior-inner process. The posterior process may develop another denticulation just at the outer-posterior extremity, with a maximum of three primitive denticles or nodes (Pl. 2, fig. 5).

Remarks. If compared with the platforms of *Amorphognathus ordovicicus* and *A. superbus*, *Amorphognathus?* sp. appears primitive both in denticulation and in disposition of the processes, and it is more similar to older species of the genus such as *A. inaequalis*. The platforms described above could also represent, as suggested by Bergström (pers. comm. 1993), the non-blade element of *Sagittodontina robusta*. All the types reported here are also present in the upper Ordovician of Spain (Ferretti 1992).

Occurrence. Upper Ordovician of Thuringia and Spain.

Genus SAGITTODONTINA Knüpf, 1967

Type species. *Sagittodontina robusta* Knüpf, 1967.

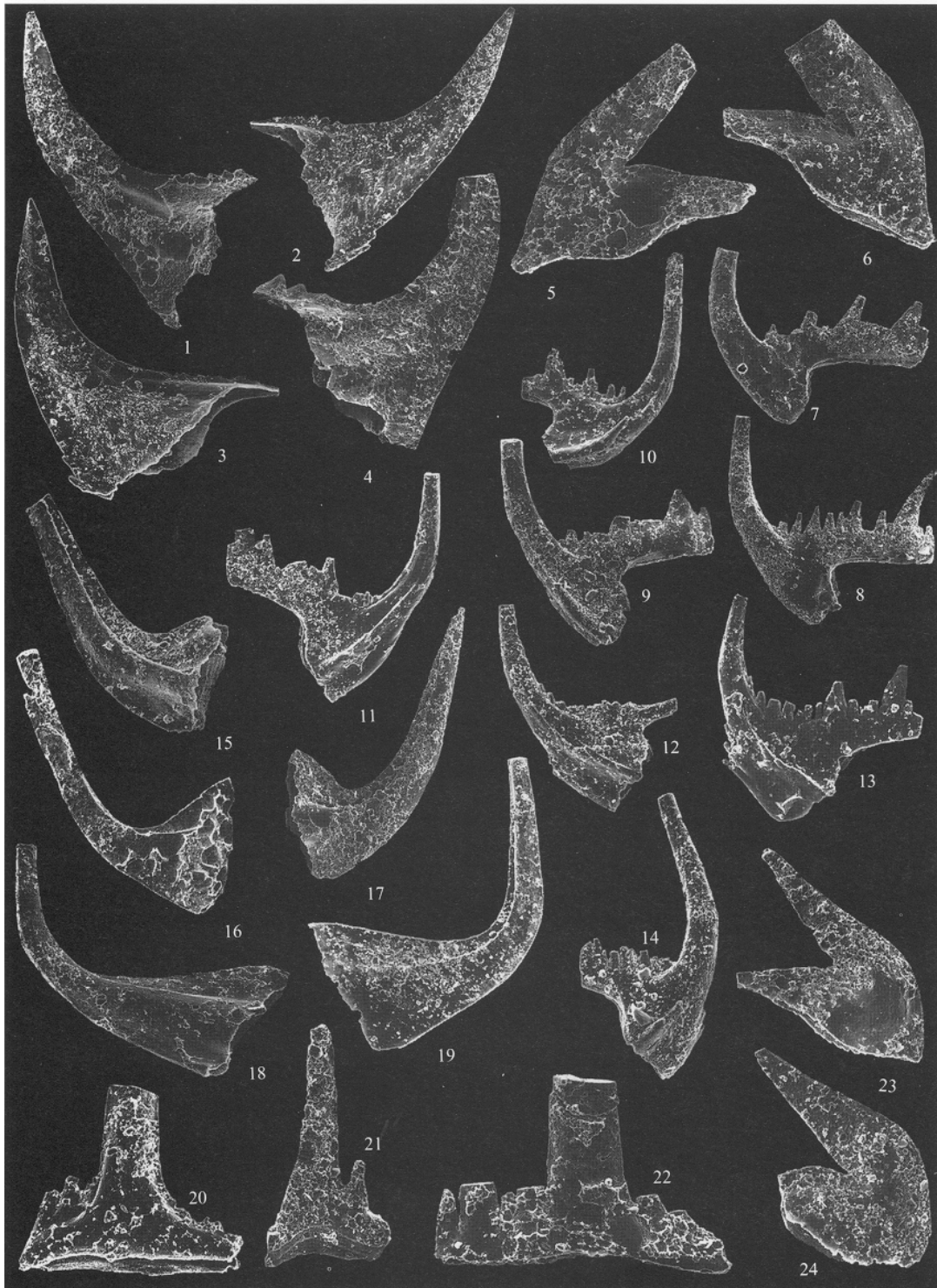
Sagittodontina robusta Knüpf, 1967

Plate 4, figures 1–23

- 1967 *Sagittodontina robusta* Knüpf, p. 38, pl. 8, figs 3a–b, 4.
 1967 *Sagittodontina separata* Knüpf, p. 38, pl. 8, figs 5, 7a–b.
 1967 *Sagittodontina unidentata* Knüpf, p. 39, pl. 8, figs 1a–b, 2a–b.
 1967 *Sagittodontina bifurcata* Knüpf, p. 39, pl. 7, fig. 5a–b.
 1967 *Sagittodontus dentatus* (Ethington); Knüpf, p. 37, pl. 7, fig. 6a–b.
 ?1967 *Sagittodontus robustus robustus* Rhodes; Knüpf, p. 36, pl. 4, fig. 7a–b; pl. 5, fig. 9a–c.
 ?1967 *Sagittodontus robustus flammeus* Knüpf, p. 37, pl. 5, fig. 8a–b; pl. 11, figs 9–10.
 1967 *Zygognathus ?atypica* Knüpf, p. 43, pl. 5, figs 5a–b, 7a–b.
 ?1967 *Acodus deltatus altior* Lindström; Knüpf, p. 17, pl. 4, figs 2–6.
 1967 *Ligonodina ?sp.* Knüpf, p. 33, pl. 4, fig. 14.
 1967 *Strachanognathus thuringensis* Knüpf, p. 40, pl. 5, fig. 6a–b.
 1967 *Zygognathus asymmetrica* Knüpf, p. 42, pl. 6, figs 1a–b, 2a–b.
 1967 *Trichonodella* n. sp. Knüpf, p. 41, pl. 6, figs 3a–b, 4.

EXPLANATION OF PLATE 3

- Figs 1–14. *Hamarodus europaeus* (Serpagli, 1967). 1–2, IPUM 24766; × 80; IPUM 24767; × 90; Pa elements. 3–4, IPUM 24768; × 95; IPUM 24769; × 75; Pb elements. 5–6, IPUM 24770; × 100; IPUM 24771; × 100; M elements. 7–8, IPUM 24772; × 90; IPUM 24773; × 100; Sc elements. 9–10, IPUM 24774; × 100; IPUM 24775; × 100; Sa elements. 11, IPUM 24776; × 115; Sb element. 12–14, IPUM 24777; × 120; IPUM 24778; × 140; IPUM 24779; × 120; Sd elements. All lateral views.
 Figs 15–19. *Dapsilodus mutatus* (Branson and Mehl, 1933). 15, IPUM 24780; × 100. 16, IPUM 24781; × 105. 17, IPUM 24782; × 85. 18, IPUM 24783; × 115. 19, IPUM 24784; × 110. All lateral views.
 Figs 20–22. ‘carniodiform’ elements. 20, IPUM 24785; × 145. 21, IPUM 24786; × 100. 22, IPUM 24787; × 150. All lateral views.
 Figs 23–24. ‘oistodiform’ elements. IPUM 24788; × 100. IPUM 24789; × 130. Both lateral views.



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- 1967 *Tripodontus muelleri* Knüpfer, p. 42, pl. 6, figs 5a–b, 6a–b.
 1967 *Tripodontus compactus* Knüpfer, p. 41, pl. 6, figs 7, 8a–b.
 1967 *Distacodus stola* Lindström; Knüpfer, p. 25, pl. 5, figs 1a–b, 2.
 1967 *Goniodontus ordovicicus* Knüpfer, p. 29, pl. 4, figs 8, 9a–b, 10; pl. 11, fig. 11.
 1967 *Goniodontus* n. sp. Knüpfer, p. 29, pl. 4, fig. 13.
 ?1967 *Acodus abnormis* Knüpfer, p. 17, pl. 3, figs 9, 13a–b.
 1967 *Roundya gebersdorfi* Knüpfer, p. 35, pl. 4, figs 11–12.
 1967 *Clavohamulus* n. sp. 1 Knüpfer, p. 23, pl. 1, figs 1a–b, 2a–b.
 1967 *Clavohamulus* n. sp. 2 Knüpfer, p. 23, pl. 1, figs 3a–c.
 1967 *Lonchodus* sp. Knüpfer, p. 34, pl. 8, figs 8–9.
 1982 *Sagittodontina robusta* Knüpfer; Paris *et al.*, p. 21, pl. 2, fig. 11; pl. 3, figs 1–3, 5; pl. 4, figs 1–2, 4, 6.
 1983 *Sagittodontina bifurcata* Knüpfer; Bergström, fig. 4.
 1990 *Sagittodontina robusta* Knüpfer; Fuchs, p. 206, pl. 5, figs 1–8; pl. 7, fig. 1.
 ?1990 *Rhodesognathus elegans* (Rhodes); Fuchs, p. 206, pl. 6, fig. 4.
 1992 *Sagittodontina robusta* Knüpfer; Bergström and Massa, p. 1338, pl. 1, figs 6–8, ?9, 10–14, 17.

Description. Pa elements of morphogenus ‘*Sagittodontina* Knüpfer, 1967’ with cusp slightly inclined posteriorly. The anterior process carries up to five rounded denticles which are suberect or with same inclination as cusp. Denticles are independent of each other. Bifurcation of denticles on posterior process may form immediately posterior to cusp or another denticle, commonly with an opposite inclination to cusp. Two gentle costae, along which denticles of posterior process develop, converge and extend to cusp (Pl. 4, fig. 23). No complete specimens have been found, so nature of posterior part is uncertain, but two rows of denticles on the process could have developed more or less parallel and not necessarily connected to each other. Various fragments classified by Knüpfer (1967) as ‘*Lonchodus* sp.’ may have occupied this element position (Pl. 4, fig. 22). No oral edge has been observed on the platform. The lateral process can be long and weakly denticulated, carrying a maximum of two denticles. A very deep basal cavity is common to all denticles. The denticulation of the anterior process of ‘*Sagittodontus dentatus* Knüpfer, 1967’ is more a crenulation of its anterior margin. The platform-like posterior process shows only the posterior part of a narrow and flat area with no visible denticles (Pl. 4, fig. 1) or one small denticle (Pl. 4, fig. 4). As in the previous morphogenus, two lines converge and extend to the cusp.

Pb elements are well preserved and are represented only by sinistral forms.

In a few M elements, the cusp appears to split into two small denticles. The posterior process is denticulated and partially preserved only in one specimen (Pl. 4, fig. 12).

S elements (Pl. 4, figs 13–20) are clearly distinguishable, even as fragments, by their cross section: triangular in the Sa and Sb position, but with different symmetry, and square in the Sd.

All the elements of our fauna have a very pale colour, on account of their limited wall thickness, and are extremely fragile.

Remarks. *Sagittodontina robusta* is one of the dominant components of our fauna, with well preserved specimens. Thuringia appears to be the best source of specimens of this species. Only elements included by Knüpfer (1967) in the morphogenus ‘*Sagittodontina*’ (‘*S. bifurcata*’, ‘*S. unidentata*’, ‘*S. robusta*’, ‘*S. separata*’) and in the morphospecies ‘*Sagittodontus dentatus* Ethington, 1959’ develop a platform-like posterior process distally from the cusp, although it is never completely preserved. ‘*Sagittodontus robustus robustus* Rhodes, 1953’ and ‘*Sagittodontus robustus flammeus* Knüpfer, 1967’ retain their pyramidal shape with no denticles or platform-like expansions (Pl. 4, fig. 9). As they are not complete, it is possible that they could have developed a platform similar to the one described for ‘*S. dentatus* Ethington, 1959.’

Surprisingly, only sinistral ‘ambalodiform’ elements occur (Pl. 4, figs 5–7), as independently noted by Stouge (pers. comm. 1993). In contrast, only dextral forms of another ‘ambalodiform element’, previously considered to belong to *Rhodesognathus elegans*, are present (Pl. 2, figs 11–13). It is possible that they belong in the same apparatus, even if not mirror images, and not necessarily in *Sagittodontina robusta*. Fragments classified as ‘*Clavohamulus* n. sp. 1 and 2’ by Knüpfer (1967) are probably part of ramiform lateral processes, as they are small and always broken (Pl. 4, fig. 21).

Occurrence. Upper Ordovician of Thuringia, Spain, north-west France, ?Bohemia and Libya.

Family ICRIODELLIDAE Sweet, 1988

Genus ICRIODELLA Rhodes, 1953

Type species. Icriodella superba Rhodes, 1953.

Icriodella sp.

Plate 1, figure 16

Description. Only one fragment of a Pa anterior process has been found in our fauna. The node-like denticles are slightly asymmetrical posteriorly in respect to the axis of the process. A median longitudinal ridge with a 'zigzag' pattern runs along the median part of the process. Sides are narrow and the basal cavity deep.

Remarks. This distinctive fragment may represent a new species of *Icriodella*, but owing to its scarcity in our fauna we have preferred to leave it in open nomenclature.

Order PROTOPANDERODONTIDA Sweet, 1988

Family ACANTHODONTIDAE Lindström, 1970

Genus CORNUODUS Fähræus, 1966

Type species. Cornuodus erectus Fähræus, 1966.

Cornuodus longibasis (Lindström 1955)

Plate 2, figures 18–20

- 1966 *Cornuodus erectus* Fähræus, p. 20, pl. 2, fig. 8a–b; text-fig. 2b.
- 1974 '*Cornuodus*' *longibasis* (Lindström); Serpagli, p. 43, pl. 7, fig. 2a–b; pl. 20, fig. 12.
- 1978 *Cornuodus longibasis* (Lindström); Löfgren, p. 49, pl. 4, figs 36, 38–42; text-fig. 25A–C.
- 1990 *Cornuodus longibasis* Lindström; Stouge and Bagnoli, p. 14, pl. 3, figs 3–7.
- 1994 *Cornuodus longibasis* Lindström; Dzik, p. 61, pl. 11, figs 8–13; text-fig. 4a.

Description. Only six specimens of this form species are present; they are not well preserved. They are bilaterally symmetrical and all with straight profile of the base. Only one (Pl. 2, fig. 18) shows longitudinal costae close to the posterior margin.

Occurrence. From the lower to upper Ordovician in Europe (Thuringia, Sweden, Poland, Russia), Korea, North and South America.

Family DREPANOISTODONTIDAE Fähræus and Nowlan, 1978

Genus DREPANOISTODUS Lindström, 1971

Type species. Oistodus forceps Lindström, 1955.

Drepanoistodus? sp.

Plate 5, figures 1–12

- ?1959 *Drepanodus* sp. Lindström, p. 439, pl. 3, figs 1–5; text-fig. 3 (3).
- 1967 *Drepanodus* n. sp. aff. *suberectus* (Branson and Mehl); Knüpfer, p. 28, pl. 2, figs 7–8.

Description. Erect (Pl. 5, figs 3–8) and suberect (Pl. 5, figs 1–2, 9–10) elements with large basal cross section. Deep basal cavity. M? elements (Pl. 5, figs 11–12) rare and with wide base.

Remarks. *Drepanoistodus?* sp. is a common species in the fauna.

Occurrence. Upper Ordovician of Germany and ?Wales.

Family PROTOPANDERODONTIDAE Lindström, 1970

Genus SCABBARDELLA Orchard, 1980

Type species. Drepanodus altipes Henningsmoen, 1948.

Scabbardella altipes (Henningsmoen, 1948)

Plate 1, figures 17–22

- 1948 *Drepanodus altipes* Henningsmoen, p. 420, pl. 25, fig. 14.
 1967 *Acodus flagellus flagellus* Knüpfer, p. 17, pl. 3, figs 5–8.
 1967 *Acodus flagellus compactus* Knüpfer, p. 18, pl. 3, figs 3–4.
 1967 *Acontiodus altipes* Knüpfer, p. 19, pl. 3, fig. 1.
 1967 *Drepanodus flagellus flagellus* Knüpfer, p. 26, pl. 2, figs 16–18.
 1967 *Drepanodus flagellus pseudoaltipes* Knüpfer, p. 26, pl. 2, fig. 11.
 1980 *Scabbardella altipes* (Henningsmoen); Orchard, p. 25, pl. 5, figs 2–5, 7–8, 12, 14, 18, 20, 23–24, 28, 30, 33, 35; text-fig. 4c.
 1991 *Scabbardella altipes* (Henningsmoen); Ferretti and Serpagli, pl. 1, figs 12–14.
 1992 *Scabbardella altipes* (Henningsmoen); Bergström and Massa, p. 1339, pl. 1, figs 1, 3–4.
 1994 *Scabbardella altipes* (Henningsmoen); Dzik, p. 64, pl. 11, figs 36–39; text-fig. 6e.

Remarks. *Scabbardella altipes* is a common species in the Thuringian material. Our specimens appear variable in general profile as in length and curvature of the cusp. Both the subspecies (*S. altipes* subsp. A and B) described by Orchard (1980) are represented.

Occurrence. Upper Ordovician of Europe (Great Britain, Spain, France, Carnic Alps, Sardinia, Thuringia, Bohemia, Norway, Sweden), Libya and North America.

Order Unknown

Family Unknown

Genus ISTORINUS Knüpfer, 1967

Type species. Istorinus erectus Knüpfer, 1967.

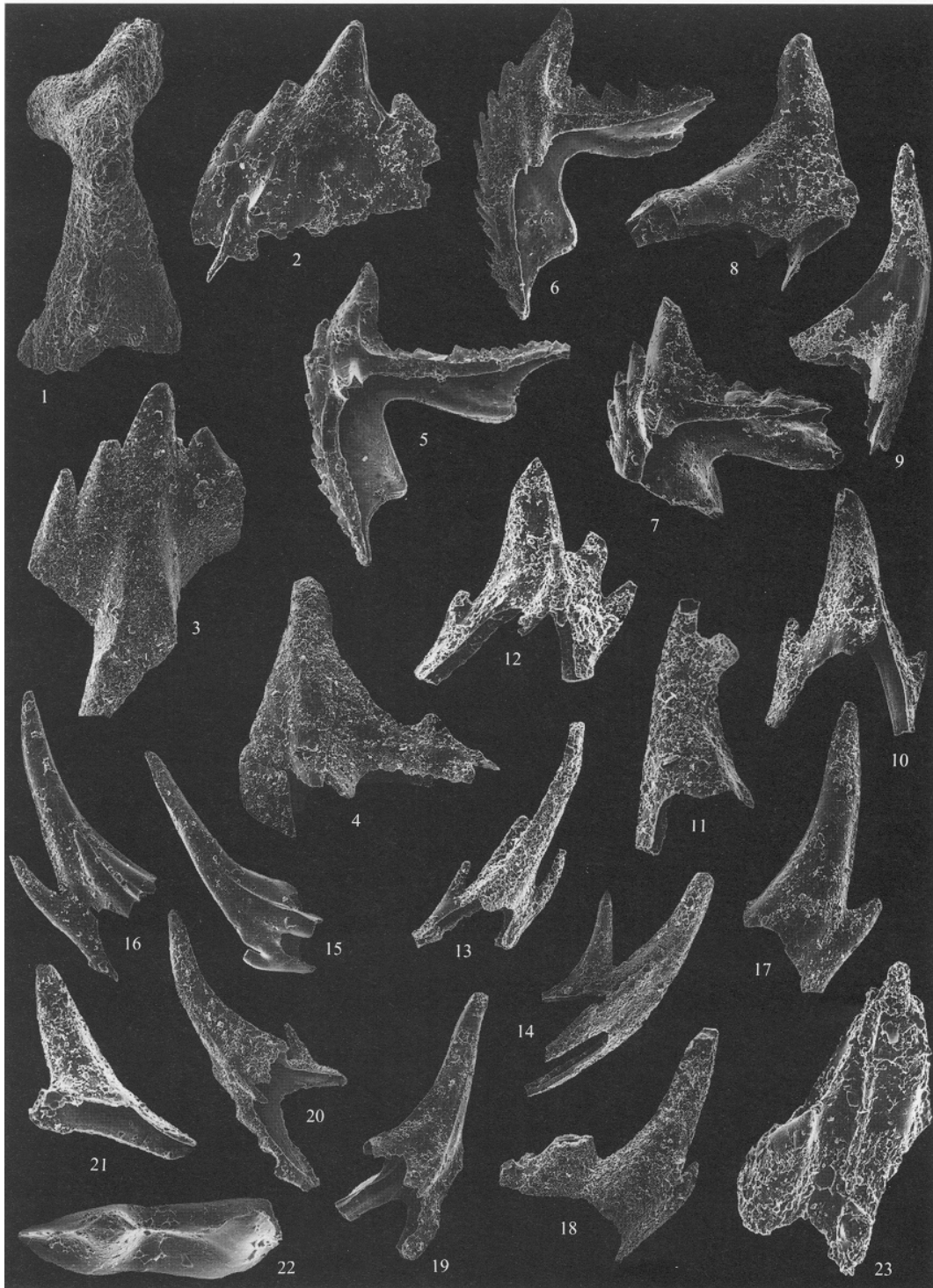
Istorinus erectus Knüpfer, 1967

Plate 5, figures 13–20

- 1967 *Istorinus erectus* Knüpfer, p. 31, pl. 1, figs 4–6.
 1967 *Istorinus postdentatus* Knüpfer, p. 31, pl. 1, fig. 10.
 1967 *Istorinus recurvus* Knüpfer, p. 32, pl. 1, figs 7–9.

EXPLANATION OF PLATE 4

Figs 1–23. *Sagittodontina robusta* Knüpfer, 1967. 1, IPUM 24790; × 90; upper view of Pa element. 2, IPUM 24791; × 80; lateral view of Pa element. 3, IPUM 24792; × 90; lateral view of Pa element. 4, IPUM 24793; × 70; lateral view of Pa element. 5–7, IPUM 24794; × 75; IPUM 24795; × 85; IPUM 24796; × 95; lateral views of Pb elements. 8–9, IPUM 24797; × 70; IPUM 24798; × 70; lateral views of Pa elements. 10–12, IPUM 24799; × 90; IPUM 24800; × 130; IPUM 24801; × 100; lateral views of M elements. 13–14, IPUM 24802; × 75; IPUM 24803; × 60; posterior and lateral views of Sa elements. 15–16, IPUM 24804; × 75; IPUM 24805; × 90; lateral views of Sb elements. 17–18, IPUM 24806; × 100; IPUM 24807; × 90; lateral views of Sc elements. 19–20, IPUM 24808; × 70; IPUM 24809; × 70; lateral views of Sd elements. 21, IPUM 24810; × 100; lateral view. 22, IPUM 24811; × 120; upper view. 23, IPUM 24812; × 145; lateral view of fragment of Pa element showing two thin costae converging to the cusp.



FERRETTI and BARNES, *Sagittodontina robusta*

- 1967 *Drepanodus disymmetricus* Knüpfer, p. 26, pl. 2, figs 1–3.
 1967 *Drepanodus humilis* Knüpfer, p. 27, pl. 2, figs 4–6.
 1992 *Istorinus erectus* Knüpfer; Bergström and Massa, p. 1338, pl. 1, figs 15–16.

Description. Multielement species of *Istorinus* composed of small, laterally compressed elements with sharp anterior and posterior margins and deep basal cavity expansive in lower two-thirds of cusp and under denticles. Lateral faces are smooth. Denticles are generally present only on one side of cusp, being completely independent from cusp or partially fused with its basal portion. Walls are very thin, hence their pale colour. The cusp is erect to suberect. Three main element morphotypes have been recognized in our fauna.

The first type (Pl. 5, figs 13–14) has a simple triangular shape with wide base. A small denticle is commonly present on the steeper side of the cusp.

In the second type (Pl. 5, figs 15, 17–18), which is probably the most familiar form of *Istorinus*, the basal margin is straight and of variable length. The general profile of the element in lateral view is asymmetrical, having anterior and posterior margins with different curvature, one gentle, the other sharp. One or two denticles, developed parallel or slightly divergent to the cusp axis, are present on the latter edge and may extend to half cusp height. All our specimens bearing two denticles are broken, hence additional denticles may have been present. The gentle margin of the element can be long, being undenticulated or carrying a small denticle at its extremity (Pl. 5, fig. 15). A common deep basal cavity extends under the cusp and each denticle.

The third type (Pl. 5, figs 16, 19) shares the same denticulation, but the basal margin is arched below the cusp. In some specimens, it may be flexed differently in two lateral faces, leaving visible the basal margin of the opposite one.

Remarks. Dzik (1989) suggested that *Istorinus erectus* may simply represent the process fragments of ramiform elements of *Sagittodontina robusta*. Bergström and Massa (1992) noted that their specimens from the upper Ordovician of Libya appear to be complete. Our specimens are also complete (Pl. 5, figs 16b, 20), and many are clearly too large to be parts of the ramiform processes. Nevertheless, some posterior processes of the S elements in *Sagittodontina robusta* are close morphologically, especially to the second morphotype described above.

Occurrence. *Istorinus erectus* is known in the upper Ordovician of Thuringia, Spain, north-west France and Libya.

'ambalodiform' element

Plate 2, figures 11–13

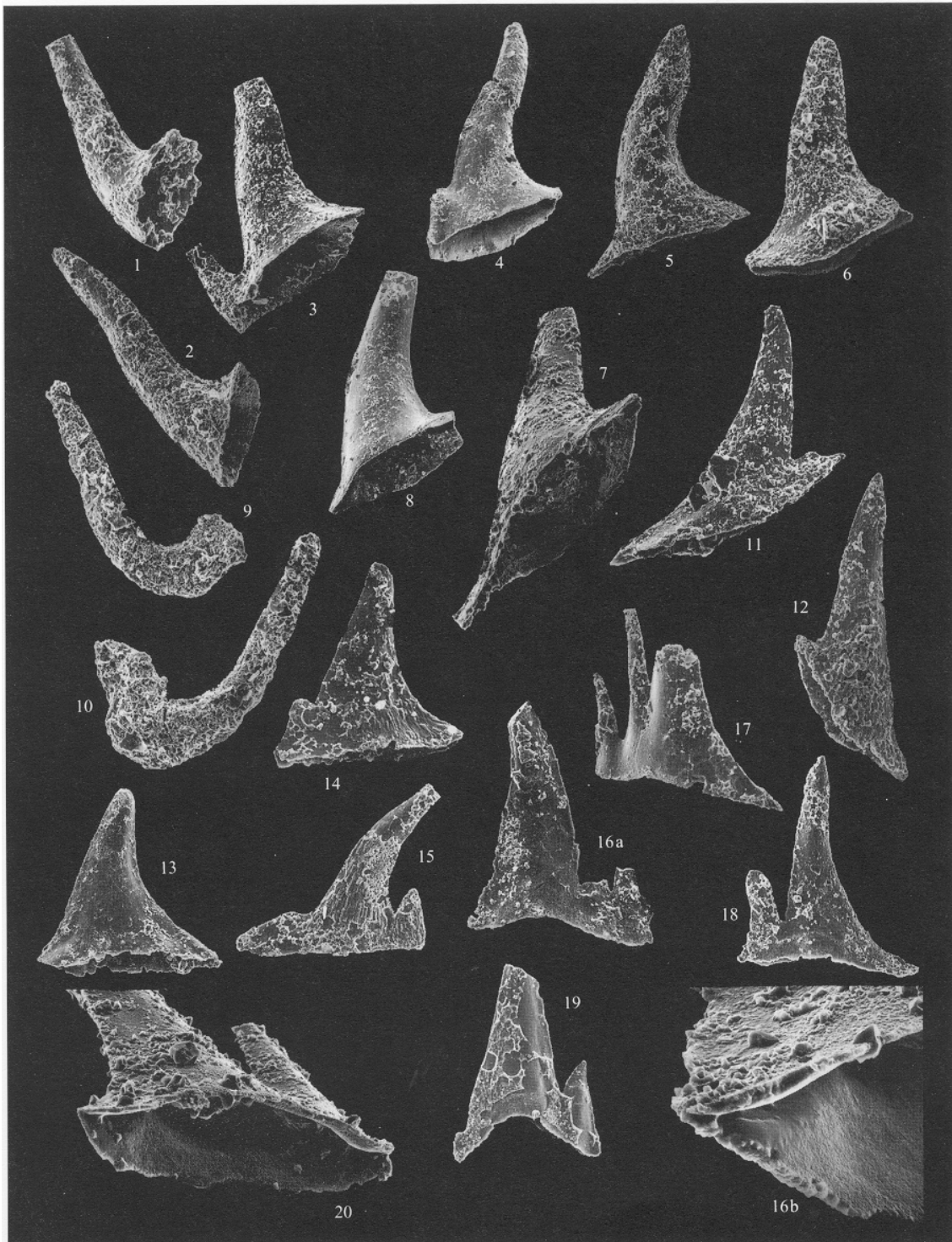
- 1967 *Ambalodus triangularis triangularis* Branson and Mehl; Knüpfer, p. 20, pl. 9, fig. 2a–b.

Description. These 'ambalodiform' elements are characterized by a very long, straight and slender denticulated anterior bar. The posterior bar is denticulated and of a different width, being slender or wide. The outer lateral process is not denticulated or carries a single small denticle. Only dextral forms are known.

Remarks. We noted above how these forms do not conform to the features of the Pb element of *Rhodesognathus elegans*. A similar element was included by Savage and Bassett (1986) in

EXPLANATION OF PLATE 5

- Figs 1–12. *Drepanoistodus?* sp. 1, IPUM 24813; × 110; 2, IPUM 24814; × 110; 3, IPUM 24815; × 115; 4, IPUM 24816; × 85; 5, IPUM 24817; × 100; 6, IPUM 24818; × 140; 7, IPUM 24819; × 150; 8, IPUM 24820; × 95; 9, IPUM 24821; × 115; 10, IPUM 24822; × 105; 11, IPUM 24823; × 170; 12, IPUM 24824 × 160; all lateral views.
 Figs 13–20. *Istorinus erectus* Knüpfer, 1967. 13–14, IPUM 24825; × 105; IPUM 24826; × 120; lateral views. 15, IPUM 24827; × 120; lateral view. 16a–b, IPUM 24828; × 120; × 650; lateral and close oral views. 17, IPUM 24829; × 135; lateral view. 18, IPUM 24830; × 115; lateral view. 19, IPUM 24831; × 120; lateral view. 20, IPUM 24832; × 280; oral view.



FERRETTI and BARNES, *Drepanoistodus?*, *Istorinus*

Amorphognathus superbus, but as the diagnostic M elements of this species are absent in our material, assignment to *A. superbus* is unlikely. They have been reported also from Spain (Ferretti 1992).

Occurrence. Upper Ordovician of Thuringia and Spain.

‘carniodiform’ element

Plate 3, figures 20–22

- 1955 ‘indeterminate fragment’ Rhodes, pl. 8, fig. 11; pl. 9, fig. 7.
 ?1964 ?*Prioniodina aflexa* Hamar, p. 277, pl. 3, figs 15, 18–19; text-fig. 5.
 1967 ‘*Carniodus*’ sp.; Serpagli, p. 56, pl. 22, figs 1–3.
 1967 *Carniodus* sp. Walliser; Knüpfer, p. 22, pl. 8, figs 6, 10–12.
 1980 *Eocarniodus gracilis* (Rhodes); Orchard, p. 20, pl. 2, figs 19, 30–31, 36.
 1982 *Carniodus* sp. Walliser; Paris *et al.*, p. 20, pl. 2, fig. 14.

Description. Narrow, small elements that develop two processes with up to five irregular denticles that each extend from prominent central cusp. Processes may be completely aligned (Pl. 3, figs 20, 22) or flexed in an arc (Pl. 3, fig. 21). The narrow basal cavity tends to widen slightly under the cusp only in straight specimens.

Remarks. The preservation of our material is not good, and the basal ledge that is visible in some elements from Britain (Orchard 1980, pl. 2, fig. 19) has rarely been observed. No complete specimens are present in our collection and we have preferred a morphospecific description. This does not exclude the possibility that they may belong to *Eocarniodus gracilis* Orchard, 1980.

Broken bars of ramiform elements of *Amorphognathus* have been confused with these elements. This could have occurred also with the ramiform elements of *Hamarodus europaeus*, which are bigger and closer in size to our specimens. Nevertheless, in no bar of either species did we note the characteristic flexure of the two processes of some elements included here.

Occurrence. ?Caradoc and Ashgill of Great Britain, Spain, Bohemia, France, Norway, Sardinia, Carnic Alps and Thuringia; lower Silurian of the Carnic Alps.

‘oistodiform’ element

Plate 3, figures 23–24

- ?1967 *Oistodus abundans* Branson and Mehl; Knüpfer, p. 34, pl. 5, fig. 3.

Remarks. Compared with *Oistodus niger* Serpagli, 1967, the M element of *Hamarodus europaeus*, some ‘oistodiform’ elements in our fauna are smaller and have a more recurved anterior margin. They also lack the slight concavity of the basal margin at the anterior extremity (the basal margin is therefore convex and only posteriorly concave) and have a more reclined aspect overall. As great variability has been noted above for the corresponding M element of *Hamarodus europaeus*, it is still possible that they may be an extreme variant within the latter species.

Gen. et sp. indet.

Plate 2, figure 21

Description. Weakly arched and flexed blade element with subcentral low cusp, a posterior denticulated process and an anterior denticle. Anterior inner process complete and gently expanding in a ridge.

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