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Iapetonudus (N. gen.) and *Iapetognathus* Landing, Unusual Earliest Ordovician Multielement Conodont Taxa and Their Utility for Biostratigraphy

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ABSTRACT

The Early Ordovician (Tremadocian) multielement conodont genus *Iapetognathus* is one of the oldest denticulate euconodont genera known. The ramiform-ramiform apparatus structure of *Iapetognathus* is not similar morphologically to other Late Cambrian to Earliest Ordovician denticulate multielement taxa, such as *Eodentatus* or *Cordylodus*, because the major denticulate process has a lateral rather than a posterior orientation as it is in the other two examples. For this reason the genus is believed to have developed from the coniform-coniform apparatus *Iapetonudus ibexensis* (N.gen., n.sp.) through the development of the denticulate lateral processes. The two genera have a number of morphologic features in common and appear in stratigraphic succession.

Iapetognathus aengensis (Lindström) is redefined as a multielement taxon using topotype material and *Ig. preaengensis* Landing is placed in synonymy with it. *Iapetognathus sprakersi*, recently described by Landing in Landing and others (1996), is recognized as a multielement species and the new multielement species, *Ig. fluctivagus*, *Ig. jilinensis* and *Ig. landingi* n. spp. are described herein, based on type specimens from Utah (U.S.A.), Jilin (China) and Colorado (U.S.A.) respectively.

Iapetonudus and *Iapetognathus* are important genera in defining the level of the Cambrian-Ordovician boundary. *Iapetonudus* is currently recognized only from Utah, Texas and Oklahoma, but *Iapetognathus* is cosmopolitan in its distribution.

INTRODUCTION

In deliberations for the selection of a Cambrian-Ordovician boundary stratotype section, stratigraphic intervals and their faunal components have been examined from around the world (Norford, 1982, 1988). Conodonts, graptolites and trilobites emerged as the principal groups on which to define the boundary level. Early attempts to use

species of the conodont genus *Cordylodus* Pander (1856) for characterizing this boundary (Barnes, 1988, Miller, 1988) proved difficult because of disagreement in the literature regarding definition of some key species and because of the complexity of *Cordylodus* evolution near the boundary level. The genus *Iapetognathus* also first appears at about the proposed boundary level and has a

distinctive morphology. It was thought that a species of the genus might prove useful in establishing the base of the Ordovician. In order to clarify its biostratigraphic utility, we found it necessary to develop rigorous definitions of the genus, its species, and their evolutionary relationships and stratigraphic context.

Iapetognathus is one of three latest Cambrian and earliest Ordovician euconodont genera to include multidenticulate elements, the others being *Cordylodus* Pander and *Eodentatus* Nicoll and Shergold (1991). The development of denticulation in conodonts was achieved in several ways by different genera (Nicoll 1990, 1992). In both *Eodentatus* and *Cordylodus*, denticle development was initiated on a posterior process located in the plane of the cusp. However, in *Iapetognathus*, using the curvature of the cusp and the shape and tip position of the basal cavity for orientation, the processes are directed laterally rather than posteriorly. The analysis of latest Cambrian and earliest Ordovician conodont genera, their apparatus structure, and their stratigraphic and geographic distribution has received considerable attention in recent years, but many details remain to be worked out. The genera *Cordylodus* and *Eodentatus* have been the subject of much recent analysis (Miller, 1980, 1984, 1988; Miller and Stitt, 1995; Nicoll, 1990, 1991; Nicoll and Shergold, 1991). However, aside from brief discussions by Barnes (1988) and Landing and others (1996), *Iapetognathus* has not been studied in detail since it was established by Landing in Fortey and others (1982). Landing in Landing and others (1996) presented a brief description of a new species, *Ig. sprakersi*.

The genus *Iapetognathus* comprise five valid species: *Ig. aengensis* (Lindström, 1955), *Ig. sprakersi* (Landing and others, 1996) and three new species named and described herein, *Ig. fluctivagus* n. sp., *Ig. jilinensis* n. sp., and *Ig. landingi* n. sp. During this investigation we have examined the type specimens and additional topotype material of *Ig. aengensis* (Lindström) from Sweden (Lindström, 1955) and of *Ig. preaengensis* Landing from Newfoundland, Canada (Landing in Fortey and others, 1982), and we conclude that these species are synonymous. We have also examined new material of this genus from localities in the United States (Alaska, Nevada, Utah, New Mexico, Colorado, Texas, Oklahoma, Virginia, Maryland, Pennsylvania), Canada (Newfoundland), Norway (Oslo Fjord), Russia (Siberia), Kazakhstan (Malyi Karatau Range), China (Jilin) and Australia (Queensland). Additional occurrences are known from the published literature. All occurrences are documented in Tables 1–5.

In the course of this study we have discovered the apparent ancestor of *Iapetognathus*, that we describe as *Iapetonudus ibexensis* (N.gen., n.sp.) Occurrences of this species are documented in Table 6. The coniform-coni-

form apparatus of this new species developed into the characteristic ramiform-ramiform apparatus of *Iapetognathus* with the development of denticulation on lateral processes. The two genera have a number of morphologic features in common. We present a preliminary interpretation of the evolutionary relationships between *Iapetonudus* n. gen. and *Iapetognathus* and among species of *Iapetognathus* based on analysis of their biostratigraphic and morphologic relationships.

MATERIAL

CHINA

This study began with a re-examination of the conodonts in the Cambrian-Ordovician boundary interval at the Dayangcha section (latitude 42°03'40"N; longitude 126°42'25"W), Jilin, China (Nowlan and Nicoll, 1995; see also Chen and others, 1988). The section comprises a reasonably well exposed succession of the Fengshan and Yeli formations that dips at about 30° SSE. The sediments are mainly fine grained consisting of thin beds of calcareous mudstone and siltstone with locally abundant glauconite and thin beds of lime mudstone. This background sedimentation, presumably taking place in relatively deep water, is locally interrupted by deposition of flat pebble conglomerates which may represent tempestites. The main features of the section have been described in some detail by Chen and others (1988). New collections were made in 1992 and 1994 and the authors also have had access to the original collections of Chen Jun-yuan (Chen and Gong, 1986) and Zhao Da (Duan, An and Zhao, 1986). All this material was remounted and sorted, so that it could be compared more readily and a high degree of consistency in the abundance and taxonomic content in each of the data sets was recorded. During this study, the presence of specimens of *Iapetognathus* from Dayangcha was noted for the first time. The specimens from this section are assigned to *Iapetognathus jilinensis* n. sp., a species that has not been recorded from any other locality.

NEWFOUNDLAND

Once *Iapetognathus* was recognized in China, other sections containing *Iapetognathus* specimens were sought. Dr. C.R. Barnes (University of Victoria) kindly allowed us the opportunity to examine his collections from Green Point, Newfoundland (Barnes, 1988). Strata that include the Cambrian-Ordovician boundary interval at the Green Point section in Newfoundland are referred to the Cow Head Group, which was deposited near the base of the continental slope on the eastern margin of Laurentia. We were able to examine most samples from beds 19 through 37 (see Barnes, 1988, Fig. 9, Table 6). Sample 28, from the

base of the Broom Point Member of the Green Point Formation, is the lowest sample reported by Barnes (1988) with specimens of *Iapetognathus* and this sample also contains the first occurrence of *C. lindstromi* sensu Barnes 1988. Our study indicates that the species identified as *C. lindstromi* by Barnes (1988) is, in fact, more appropriately assigned to *C. prion* Lindström. Although, nine specimens of *Iapetognathus* are reported from sample 28 in Table 6 (Barnes, 1988), only one specimen of *Iapetognathus* was identified [by GSN] in this restudy. As a result, Felicity O'Brien (Memorial University of Newfoundland) returned to the section and made additional collections. Four specimens of *Iapetognathus fluctivagus* were recovered from the sample 28 level. Among Barnes' collections, additional specimens of *Iapetognathus fluctivagus* occur in sample 30, which is thirty centimetres higher within the lower part of unit 23. Specimens of *Iapetognathus aengensis* are illustrated by Barnes (1988) from higher in this section.

WESTERN UTAH (IBEX)

Lower Ordovician strata in the Ibex area of Utah are referred to several formations within the Pogonip Group, of which the lowest is the House Limestone (Hintze, 1951, 1973; Miller and others, 1982). These strata were deposited on a tropical miogeoclinal carbonate platform. Ross and others (1993, 1997), in documenting and defining the Ibexian Series stratotype and its subdivisions, erected the *Iapetognathus* Zone between the *Cordylodus lindstromi* and *Cordylodus angulatus* Zones, with its base coinciding with the first appearance of *Iapetognathus*, at 42.7 m (140 ft) above the base of the House Limestone at the Lava Dam North section. The lower member of the House Limestone is well displayed at the Lawson Cove Section (Fig. 1) where elements of *Iapetonudus ibexensis*, *Iapetognathus fluctivagus*, *Ig. sprakersi*, and *Ig. aengensis* occur from 50.3 m to 86.9 m above the base of the unit. Abundant material from this section and related sections in the Ibex area provided many of the specimens of *Ig. fluctivagus* and *Ig. sprakersi* used for description of those species. The section also provided most of the specimens of *Iapetonudus*.

TEXAS-OKLAHOMA

Much of the additional material for this study is from Lower Ordovician strata in the Llano Uplift in central Texas and the Wichita Mountains area in southwestern Oklahoma. Texas strata containing *Iapetonudus* and *Iapetognathus* are assigned to the San Saba Member of the Wilberns Formation and the overlying Threadgill Member of the Tanyard Formation (Miller and others, 1982; Miller, 1987; Miller and Stitt, 1995). Equivalent strata in Oklahoma are assigned to the Signal Mountain Limestone and the overlying McKenzie Hill Limestone

(Miller and others, 1982). The Signal Mountain Limestone produced the first elements of the species that is described herein as *Iapetognathus fluctivagus* n. sp., which Miller (1970) found during research for his dissertation.

GEOGRAPHIC AND FACIES DISTRIBUTION OF *IAPETONUDUS*

Iapetonudus ibexensis is a rare species that appears to have a limited geographic and stratigraphic distribution (Table 6; references for stratigraphic sections and data concerning *Iapetonudus* elements contained therein are cited in the table; stratigraphic range is shown on Fig. 1). Utah strata are miogeoclinal platform carbonates, Texas strata are cratonic platform carbonates, and Oklahoma strata are shallow water limestones deposited in an aulacogen. This distribution suggests the species was adapted to low-latitude, shallow marine conditions.

GEOGRAPHIC AND FACIES DISTRIBUTION OF *IAPETOGNATHUS*

Iapetognathus has a cosmopolitan distribution at the generic level, although some species are not widely distributed (Fig. 2). Occurrences of *Iapetognathus aengensis*, *Ig. fluctivagus*, *Ig. landingi*, and *Ig. sprakersi* are summarized and referenced in Tables 1–4, and occurrences of *Iapetognathus* spp. are summarized and referenced in Table 5. No such table is presented for *Ig. jilinensis* because it has very limited distribution, as discussed below. *Iapetognathus* occurs in North America (eastern and western Canada; several parts of the U.S.A., including Alaska), South America (Argentina), Europe (Estonia, Norway, Sweden), Asia (China, Kazakhstan, eastern Siberia), Australia (Queensland, Tasmania), and possibly Antarctica (Victoria Land). The number of occurrences is likely to increase as other specialists become more familiar with the genus and as other regions come under study for conodonts. The geographic and facies distribution of each species is considered separately.

Iapetognathus aengensis occurs in northern Europe, Australia, and several parts of North America (Table 1). Localities include a variety of lithologies representing various depositional environments, including high-latitude platform limestones and shales in Sweden and Norway, siliciclastic facies in Estonia, continental slope deposits in Newfoundland, Quebec, and New York, tropical miogeoclinal platform carbonates in Utah, and platform carbonates in Alaska. This facies distribution suggests that *Ig. aengensis* was adapted to cold-water facies, in either high latitudes or deeper water, to a greater degree than were other species of the genus.

Iapetognathus fluctivagus occurs in a variety of marine facies in several parts of the U.S.A., eastern Canada, and

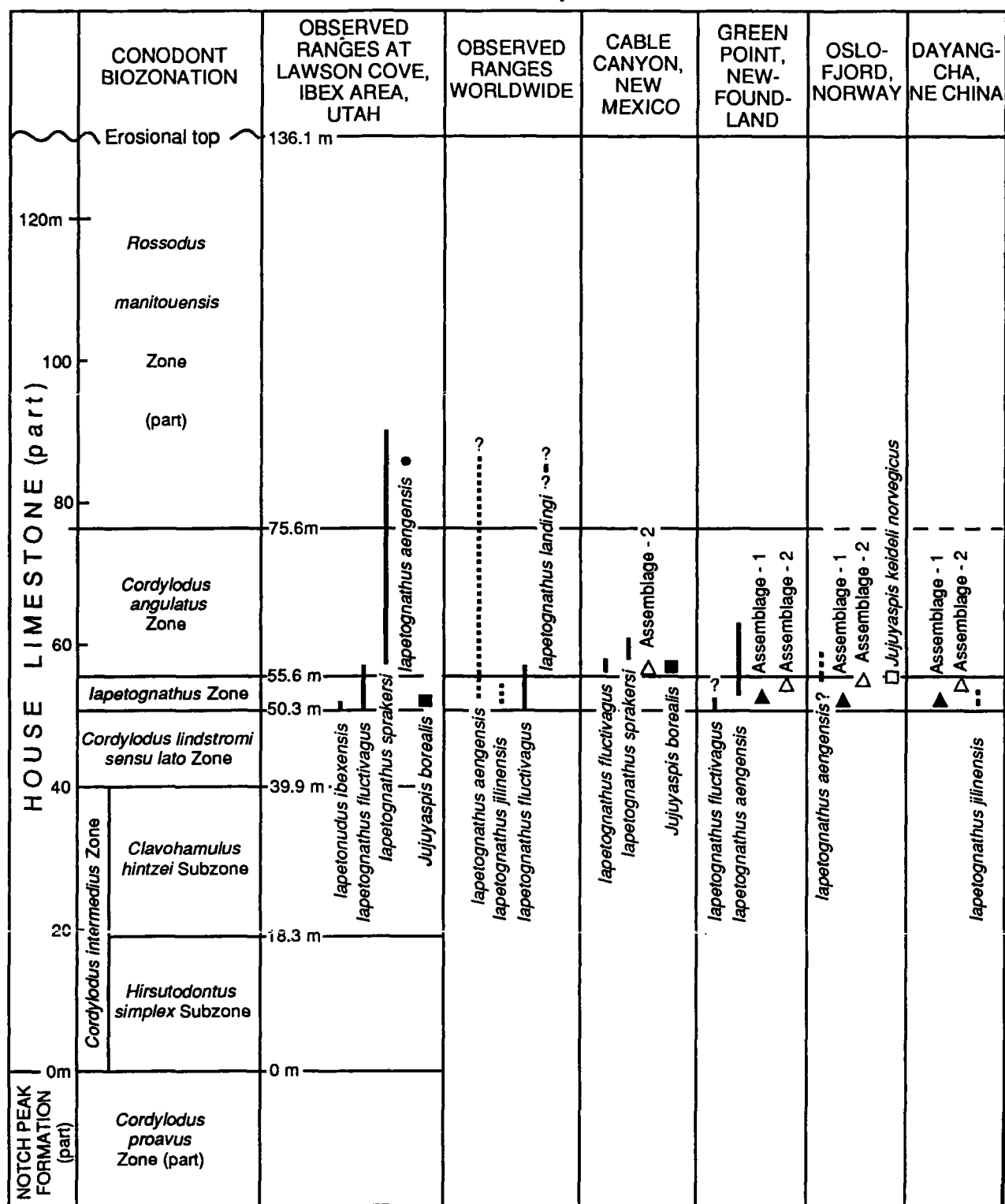


Figure 1 Stratigraphic ranges of *Iapetonodus ibexensis*, all species of *Iapetognathus* and key trilobites and graptolites. Conodont biozonation on left and ranges of species in center are based on data from the Lawson Cove section, Utah. Ranges of species on right follows Ross and others (1997); zone thicknesses and ranges of species are scaled to data from the Lawson Cove section. Triangles represent graptolite occurrences: black = Assemblage 1, open = Assemblage 2. Squares represent trilobite occurrences: black = *Jujuyaspis borealis*, open = *Jujuyaspis keideli norvegicus*.

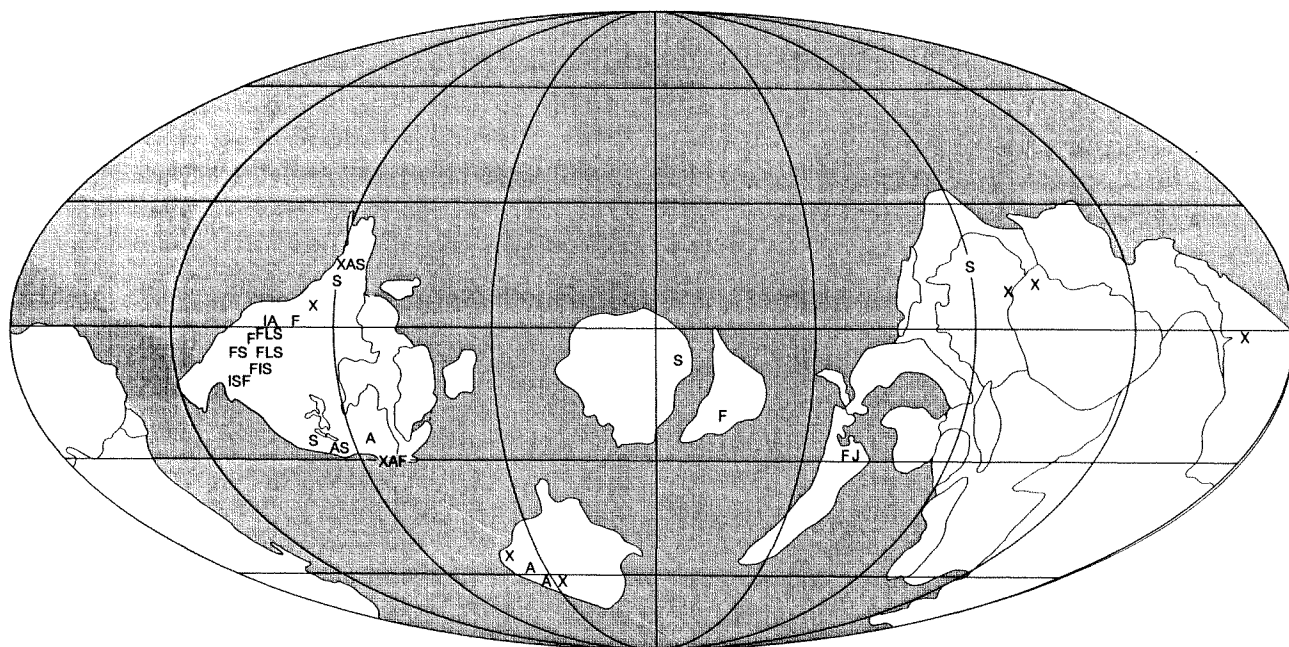


Figure 2. Paleogeographic map (based on Tremadoc map of Scotese and McKerrow, 1990) showing global distribution of species of *Iapetonudus* and *Iapetognathus*. I = *Iapetonudus ibexensis*; A = *Iapetognathus aengensis*; F = *Iapetognathus fluctivagus*; J = *Iapetognathus jilinensis*; L = *Iapetognathus landingi*; S = *Iapetognathus sprakersi*; X = *Iapetognathus* sp.

Kazakhstan (Table 2). Most of these occurrences are from relatively shallow marine environments, but *Ig. fluctivagus* also occurs in slope facies in Nevada, Newfoundland and Kazakhstan. It is common in North America, and its presence in Kazakhstan suggests that it may be more widely distributed than is presently known. Its short stratigraphic range (Fig. 1) may be a factor in its being found mostly in North America, as most of the intensive investigation of this interval has been in North American sections.

Iapetognathus sprakersi is widely distributed in North America and occurs in New York, Pennsylvania, Maryland, Virginia, Texas, Oklahoma, Colorado, New Mexico, Utah, Nevada, Alaska, and Yukon Territory (Table 4). Strata in the U.S.A. accumulated in a variety of carbonate ramp and platform, cratonic mixed carbonate/clastic, and continental slope settings. In the Red Canyon section of Nevada (locality 24, Table 4), *Ig. sprakersi* occur in a much younger conglomerate consisting of redeposited carbonate clasts, so the original depositional environment is unknown. Australian strata were deposited on a shallow marine carbonate platform. Siberian strata are platformal to cratonic mixed siliciclastic-carbonate facies (Mussa Gagiev, personal communication to Repetski). *Iapetognathus sprakersi* appears to have been adapted to warm, shallow marine conditions, although it also occurs in slope strata.

The other two species of *Iapetognathus* are known from few localities. *Iapetognathus landingi* occurs in cratonic shallow marine limestone in Colorado and in tropical miogeoclinal platform carbonates in Utah (Table 3). *Iapetognathus jilinensis* occurs only in the Fengshan Formation at the Xiaoyangqiao section near Dayangcha, Jilin Province, North China. These strata represent a deep shelf or slope environment and contain planktic graptolites.

Table 5 lists occurrences of *Iapetognathus* that we can not assign to a named species because the materials are unfigured and we have not examined them, or because the material can not be identified to species. Strata in Utah are tropical miogeoclinal carbonate platform deposits. Alaskan material is from carbonate platform deposits. The Newfoundland material is in slope deposits. The material from Argentina (unfigured) was reported as *Iapetognathus* sp. and as *Iapetognathus preaengensis*, a species that we consider to be a synonym of *Ig. aengensis*. Strata in Argentina include mixed siliciclastic-carbonate facies that include graptolite-bearing shales; these strata may be slope deposits. The Australian material occurs in mixed siliciclastic-carbonate facies. The Antarctic material is from limestone olistoliths in sandy turbidites deposited in a slope environment.

Elements from Alberta were reported as "New Genus 1" by Westrop, Landing, and Ludvigsen (1981). The

authors' brief description of their material indicates they are *Iapetognathus* elements. Landing in Fortey and others (1982) described *Iapetognathus* and noted its occurrence in these Canadian strata, which are miogeoclinal carbonate platform deposits. Based on the associated fauna (especially the trilobites *Jujuyaspis* and *Clelandia*), it is tempting to speculate that they may be *Iapetognathus fluctivagus*. None of the occurrences of *Iapetognathus* spp. appears to be from facies that were not inhabited by named species of the genus.

STRATIGRAPHIC DISTRIBUTION

Documenting the stratigraphic significance of *Iapetonudus* and *Iapetognathus* is a major goal of this report. In contrast to its wide geographic distribution, *Iapetognathus* is known from a relatively short stratigraphic interval (lower part of the Tremadocian Series). Some species have very limited stratigraphic ranges and are very useful for correlation. Another reason for their usefulness is that some species occur with trilobites and graptolites that are used to recognize the base of the Tremadocian Series (base of the Ordovician System). The lowest occurrences of *Iapetonudus ibexensis*, *Iapetognathus fluctivagus* and *Ig. jilinensis* in various sections (Fig. 1) are virtually indistinguishable from the base of the Tremadocian. For this reason the genus *Iapetognathus* is being considered by the International Working Group on the Cambrian-Ordovician Boundary to be the key taxon for characterizing the global stratotype section and point for the base of the Ordovician System. The lowest occurrences of *Iapetognathus sprakersi* and *Ig. aengensis* are somewhat higher in the Tremadocian. The two known occurrences of *Iapetognathus landingi* are even younger, yet still within the lower half of the Tremadocian Series. Redeposited elements (discussed in a later section of this report) are known from strata as young as Arenigian in Sweden and Whiterockian in Nevada.

Iapetognathus fluctivagus appears to be the oldest species of the genus. Based on morphology and stratigraphic position, we consider *Iapetonudus ibexensis* to be the ancestor of *Iapetognathus fluctivagus*. Most of the specimens of *Iapetonudus ibexensis*, *Iapetognathus fluctivagus*, and *Iapetognathus sprakersi* studied in this report are from the lower half of the House Limestone in the Lawson Cove section in the northern Wah Wah Mountains, Ibex area, Utah (Tables 2, 4, 6).

DETAILED DISTRIBUTION OF SPECIES

The Lawson Cove Section (Fig. 1) in Utah (Miller and Taylor, 1995) is a key section in documenting the stratigraphic relationship of species of *Iapetonudus* and *Iapetognathus*, because one species of the former and three

species of the latter are present. The upper part of the section is formed by the House Limestone (136 m thick) and the base of the House Limestone corresponds with the base of the *Hirsutodontus simplex* Subzone. The eroded top of the section lies within the *Rossodus manitouensis* Zone, but only about 30 m of section may be missing when compared with thicknesses in adjacent sections, e.g. 166 m at Lava Dam North (Miller and Taylor, 1995).

Iapetonudus ibexensis

Iapetonudus ibexensis has a very short stratigraphic range at Lawson Cove. It occurs in three samples, from 50.3 to 51.2 m above the base of the House Limestone (Fig. 1). This range coincides with the lowest part of the range of *Iapetognathus fluctivagus* and is in the lowest part of the *Iapetognathus* Zone. In Oklahoma this species occurs in one sample at the base of the *Iapetognathus* Zone, and in Texas it occurs in one sample 0.6 m above the base of that zone.

Iapetognathus fluctivagus

Iapetognathus fluctivagus occurs at Lawson Cove from 50.3 to 56.4 m above the base of the House Limestone; this interval includes all of the *Iapetognathus* Zone and the lowermost part of the *Cordylodus angulatus* Zone (Fig. 1). Considering that Cambrian strata are more than 3000 m thick in this part of Utah, the range of *Ig. fluctivagus* through only 6.1 m of strata is quite short. This species has similarly short ranges in other House Limestone sections in Utah and in coeval strata elsewhere. It occurs only in the *Iapetognathus* Zone and in the lower part of the *Cordylodus angulatus* Zone.

Iapetognathus fluctivagus occurs also in the Green Point Formation (part of the Cow Head Group) in Newfoundland, Canada. It occurs in the Green Point section; strata in this section were deposited at the bottom of the continental slope (James and Stevens, 1986). There, the lowest occurrence of *Iapetognathus fluctivagus*, in sample 28 in unit 23 (Barnes, 1988), is above the lowest occurrences of taxa diagnostic of the *Cordylodus intermedius* Zone, and its highest occurrence is slightly above the base of the *Cordylodus angulatus* Zone. Therefore, occurrences of *Ig. fluctivagus* at Green Point probably are equivalent in age to occurrences in the U.S.A.

Iapetognathus fluctivagus occurs in slope strata in two other areas. In Nevada it occurs in three localities in the Vinini Formation in the *Iapetognathus* Zone or in the *Cordylodus angulatus* Zone. The occurrence in Kazakhstan is based on material collected by Dubinina in Apollonov and others (1988) and Dubinina in Abdulin and others (1990) and by Miller (Table 2). Dubinina reported *Iapetognathus preaengensis* from this section. Miller's sample

Table 1. Occurrences of *Iapetognathus aengensis* Lindström

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1. *Ceratomyge Limestone	Änga Quarry, Stora Backor, Västergötland, south-central Sweden	Lindström (1955); Olgun (1987); Repetski & Nicoll, unpublished data
2. Ceratomyge Limestone	Orreholmen Quarry, Västergötland, south-central Sweden	Löfgren (1996)
3. +Cooks Brook Formation Curling Group	Northern Head and Woman Cove sections, Bay of Islands, Newfoundland	Fåhraeus & Roy (1993)
4. Maardu Member, Kallavere Formation	Tõnismägi section, Tallinn, Estonia	Kaljo et al., (1986); Kaljo et al., (1988)
5. +Broom Point Member, Green Point Formation, Cow Head Group	Broom Point South and Green Point sections, western Newfoundland, Canada	Landing in Fortey et al., (1982); Barnes (1988)
6. +Cap des Rosiers Group	Cap des Rosiers section, Quebec, Canada	Landing et al., (1986)
7. +Hatch Hill Formation	Section 9/23, Columbia County, New York, USA	Landing (1993)
8. *House Limestone	Lawson Cove section, northern Wah Wah Mts., Millard County, Utah, USA	Hintze, Taylor & Miller (1988); Miller & Taylor (1995); Miller & Nicoll, unpublished data
9. *House Limestone	Drum Mountains section, northern Drum Mountains, Juab County, Utah, USA	Stitt & Miller (1987); Miller, unpublished data
10. *?lower member, Jones Ridge Limestone	Jones Ridge, east-central Alaska, USA	Harris et al., (1995); Repetski, USGS location 11387-CO

*specimens of *Iapetognathus aengensis* Lindström from this locality have been examined by one or more of the authors of this report

+continental slope depositional environment

?species identification is questionable

USGS = United States Geological Survey

Table 2: Occurrences of *Iapetognathus fluctivagus n. sp.*

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1. *House Limestone	Drum Mountains section, northern Drum Mountains, Juab County, Utah, USA	Stitt & Miller (1987); Miller, unpublished data
2. *House Limestone	Chalk Knolls South section, Tule Valley, Millard County, Utah, USA	Miller, Stitt & Taylor (1990); Miller, unpublished data
3. *House Limestone	Section A, central House Range, Millard County, Utah, USA	Hintze (1951); Miller, unpublished data
4. *House Limestone	Sevier Lake Corral section, southern House Range, Millard County, Utah, USA	Miller, unpublished data
5. *House Limestone	Sevier Lake section, southern House Range, Millard County, Utah, USA	Miller (1969) and unpublished data
6. *House Limestone	Lava Dam North section, southern House Range, Millard County, Utah, USA	Miller (1969); Hintze (1973); Miller, unpublished data
7. *House Limestone	Lawson Cove section, northern Wah Wah Mts., Millard County, Utah, USA	Hintze, Taylor & Miller (1988); Miller, unpublished data
8. *House Limestone	Sawmill Canyon section, central Egan Range, White Pine County, Nevada, USA	Taylor, Repetski & Sprinkle (1981); Taylor, Cook & Miller (1989); Miller, unpublished data
9. *unnamed Ordovician strata	Palisades 7.5 minute quadrangle, Eureka County, Nevada, USA	Repetski, USGS location 6754-CO
10. *+?Vinini Formation	Roberts Mountains, Eureka County, Nevada, USA	Emsbo (1993, location E-S2-7); Repetski, USGS location 11410-CO
11. *+Vinini Formation	Carlin Mine Road section, Eureka County, Nevada, USA	Repetski, USGS locality 11399-CO
12. *+Vinini Formation	Swales Mountain section, Elko County, Nevada, USA	Repetski, USGS locality 11401-CO and ?11405-CO.
13. Garden City Formation	Franklin Basin section, Franklin County, Idaho, USA	Landing (1981); Landing et al., (1996)
14. *Manitou Formation	Main Elk Creek section, Garfield County, Colorado, USA	Myrow, Ethington & Miller (1995); Miller, unpublished data
15. *Signal Mountain Limestone	Chandler Creek section, Wichita Mountains, Comanche County, Oklahoma, USA	Stitt (1977); Miller et al., (1982); Derby et al., (1991) Miller, unpublished data
16. *San Saba Member, Wilberns Formation	Lange Ranch section, Llano Uplift, Gillespie County, Texas, USA	Miller et al., (1982); Miller (1987); Stitt & Miller (1987); Miller & Stitt (1995); Miller, unpublished data
17. *Bliss Sandstone	Cable Canyon section, Sierra County, New Mexico, USA	Taylor & Repetski (1995); Repetski, USGS locations 11468-CO and 11469-CO

18. *+Broom Point Member, Green Point Formation, Cow Head Group	Green Point section, western Newfoundland, Canada	Barnes (1988); Nowlan, unpublished data
19. *+Martin Point Member, Green Point Formation, Cow Head Group	Green Point section, western Newfoundland, Canada	Barnes (1988); Miller, unpublished data
20. *+Members 19 and 20 of Formation IV	Batyrbay section, Malyi Karatau Mountains, Kazakhstan	Abdulin et al., (1990); Miller, unpublished data
21. *Yehli Formation	Wushan Section, Lulong County, Hebei Province, China	Miller, unpublished data

*specimens of *Iapetognathus fluctivagus* n. sp. from this locality have been examined by one or more of the authors of this report.

+continental slope depositional environment

?species identification is questionable

USGS = United States Geological Survey

Table 3. Occurrences of *Iapetognathus landingi* n. sp.

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1. *Manitou Formation	Missouri Gulch section, Teller County, Colorado, USA	Maher (1950); Berg & Ross (1959); Seo & Ethington (1993); Ethington, unpublished data
2. *top of Ajax Dolomite or base of Opohonga Limestone	ca. 1.5 miles east of Eureka, Utah County, Utah, USA	Repetski, USGS locality 11448-CO

*specimens of *Iapetognathus landingi* from this locality have been examined by two of the authors of this report

USGS = United States Geological Survey

Table 4. Occurrences of *Iapetognathus sprakersi* Landing

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1 Tribes Hill Formation	Flat Creek section, Montgomery County, New York, USA	Landing et al., (1996, Fig. 5-3 only)
2. *Stonehenge Limestone	Bellefonte section, Centre County, Pennsylvania, USA	Taylor et al., (1992); Repetski, USGS location 11385-CO
3. *Stonehenge Limestone	St. Paul's Church section, Washington County, Maryland, USA	Taylor et al., (1992); Repetski, USGS location 11386-CO
4. *Grove Formation	Stup Farm section, Frederick Valley, Frederick County, Maryland, USA	Taylor et al., (1996); Repetski, USGS location 11300-CO
5. *Stonehenge Limestone	Narrow Passage Creek Section, Shenandoah County, Virginia, USA	Taylor et al., (1992); Repetski, USGS location 11384-CO
6. *San Saba Member, Wilberns Formation and Threadgill Member, Tanyard Formation	Lange Ranch section, Llano Uplift, Gillespie County, Texas, USA	Miller et al., (1982); Miller (1987); Stitt & Miller (1987); Miller & Stitt (1995); Miller, unpublished data
7. *Signal Mountain Limestone & McKenzie Hill Limestone	Chandler Creek section, Wichita Mountains, Comanche County, Oklahoma, USA	Miller et al., (1982); Stitt (1977); Derby et al., (1991); Miller, unpublished data
8. *Manitou Formation	Missouri Gulch section, Teller County, Colorado, USA	Maher (1950); Berg & Ross (1959); Seo & Ethington (1993); Ethington, unpublished data
9. *Manitou Formation	Main Elk Creek section, Garfield County, Colorado, USA	Myrow, Ethington & Miller (1995); Miller, unpublished data
10. *Bliss Sandstone	Cable Canyon section, Sierra County, New Mexico, USA	Taylor & Repetski (1995); Repetski, USGS location 11470-CO
11. *top Ajax Dolomite or base Opohonga Limestone	ca. 1.5 miles east of Eureka, Utah County, Utah, USA	Repetski, USGS location 11448-CO
12. *House Limestone	Weaver Canyon section, southern Deep Creek Range, Juab County, Utah, USA	Repetski, USGS location 11421-CO
13. *House Limestone	Drum Mountains section, northern Drum Mountains, Juab County, Utah, USA	Stitt & Miller (1987); Miller, unpublished data
14. *House Limestone	Chalk Knolls South section, Tule Valley, Millard County, Utah, USA	Miller, Stitt & Taylor (1990); Miller, unpublished data
15. *House Limestone	Section A, central House Range, Millard County, Utah, USA	Hintze (1951), Miller, unpublished data
16. *House Limestone	Sevier Lake Corral section, southern House Range, Millard County, Utah, USA	Miller, unpublished data

17. *House Limestone	Lava Dam North section, southern House Range, Millard County, Utah, USA	Miller (1969); Hintze (1973); Miller, unpublished data
18. *House Limestone	Lawson Cove section, northern Wah Wah Mountains, Millard County, Utah, USA	Hintze, Taylor & Miller (1988); Miller, unpublished data
19. *House Limestone	Sawmill Canyon section, central Egan Range, White Pine County, Nevada, USA	Taylor, Repetski & Sprinkle (1981); Taylor, Cook & Miller (1989); Miller, unpublished data
20. *Windfall Formation	Ninemile Canyon section, Antelope Range, Eureka County, Nevada, USA	Taylor & Repetski (1985); Repetski, USGS location 11307-CO
21. *lower Pogonip Group	drillcore in Eureka Mining District, Eureka County, Nevada, USA	Repetski, USGS location 11285-CO
22. *unassigned limestone	Bruffey Canyon area, Sulphur Spring Range, Eureka County, Nevada, USA	Repetski, USGS location 6420-CO
23. *+ Vinini Formation	Carlin Mine Road section, Eureka County, Nevada, USA	Repetski, USGS locality 11393-CO and 11400-CO
24. *+ Vinini Formation	Red Canyon section, Roberts Mountains, Eureka County, Nevada, USA	Ethington et al., (1995); Ethington, unpublished data
25. *+ ?Vinini Formation	Roberts Mountains, Eureka County, Nevada, USA	Emsbo (1993, location E-S2-7); Repetski, USGS location 11410-CO
26. *+ Vinini Formation	Cottonwood Canyon, Roberts Mountains, Eureka County, Nevada, USA	Emsbo (1993, location E-8-812); Repetski, USGS location 11417-CO?
27. *+ Vinini Formation	Swales Mountain section, Elko County, Nevada, USA	Repetski, USGS locations 9446-CO, 11401-CO, 11403-CO, 11404-CO, 11405-CO, 11409-CO
28. *+ Vinini Formation	Blue Basin Creek, Elko County, Nevada, USA	Repetski, USGS location 8824-CO
29. *+ basal Valmy Formation	Bull Run Mountains, Elko County, Nevada, USA	Repetski, USGS location 11389-CO
30. *lower member, Jones Ridge Limestone	Jones Ridge, east-central Alaska, USA	Harris et al., (1995); Repetski, USGS locality 11387-CO
31. Rabbitkettle Formation	Selwin Basin, Mackenzie Mountains, Yukon Territory, Canada	Pohler & Orchard (1990)
32. *Urdakh Formation	NW part of Fore-Kolyma Uplift, Eastern Siberia, Russia	Mussa Gagiev & Repetski, unpublished data
33. *Datson Member, Ninmaroo Formation	Black Mountain section GB 003, western Queensland, Australia	Shergold et al., (1991); Shergold & Nicoll (1992); Nicoll, unpublished data
34. *Bliss Sandstone	Cable Canyon section, Sierra County, New Mexico, USA	Repetski, unpublished data, USGS location 11470-CO

*specimens of *Iapetognathus sprakersi* from this locality have been examined by one or more of the authors of this report

+continental slope depositional environment

?species identification is questionable

USGS = United States Geological Survey

Table 5. Occurrences of *Iapetognathus* spp.
(including unfigured specimens or specimens not examined in this study or specimens that cannot be identified to species)

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1. *§top of St. Charles Formation	Crater Island section, Box Elder County, Utah, USA	Repetski, USGS location 11432-CO
2. ‡House Limestone	Shingle Pass section, Lincoln County, Nevada, USA	Sweet and Tolbert (1997)
3. ‡Survey Peak Formation	Mount Wilcox section, Alberta, Canada	Westrop et al., (1981); Landing in Fortey et al., (1982)
4. *lower member, Jones Ridge Limestone	Jones Ridge, east-central Alaska, USA	Harris et al., (1995); Repetski, USGS locations 11387-CO and 11388-CO
5. Maardu Member Kallavere Formation	Ülgase cliff section, northern Estonia	Heinsalu et al., (1987)
6. ‡Lampazar and Cardonal Formations	Vizcacha Creek and Amarilla Creek sections, northwestern Argentina	Rao & Hünicken (1995)
7. ○Caroline Creek Sandstone	Borehole at Beaconsfield, northern Tasmania, Australia	Kennedy (1971)
8. +Robertson Bay Group	northern Victoria Land, Antarctica	Burrett & Findlay (1984)
9. *#stinkstone concretions	Naersnes section, Oslo Region, Norway	Bruton et al., (1988)

*specimens examined by one or more authors of this paper and not identified to species

§transitional form between *Iapetognathus fluctuatus* and *Ig. sprakersi*

‡specimens of *Iapetognathus* sp. from this locality were reported as *Iapetognathus preaengensis*

○identified as "*Pravognathus*" *aengensis* but not figured

+Continental slope depositional environment

#identified as *Iapetognathus aengensis*

Table 6. Occurrences of *Iapetonudus ibexensis* n. gen., n. sp.

STRATIGRAPHY	SECTION AND LOCALITY	SOURCE OF INFORMATION
1. *House Limestone	Lawson Cove section, northern Wah Wah Mountains, Millard County, Utah, USA	Hintze, Taylor & Miller (1988); Miller, unpublished data
2. *San Saba Member Wilberns Formation	Lange Ranch section, Llano Uplift, Gillespie County, Texas, USA	Miller et al., (1982); Miller (1987); Stitt & Miller (1987); Miller & Stitt (1995); Miller, unpublished data
3. *Signal Mountain Limestone	Chandler Creek section, Wichita Mountains, Comanche County, Oklahoma, USA	Stitt (1977); Miller et al., (1982); Derby et al., (1991); Miller, unpublished data

**Iapetonudus* from this locality have been examined by two of the authors of this report

from the same horizon yielded elements that are assigned herein to *Ig. fluctivagus*, and another of Miller's samples 23 m lower yielded the same species. We assume that Dubinina's material is conspecific with material Miller found at the same level. The two samples that yielded *Iapetognathus* are above the lowest occurrence of *Cordylodus lindstromi* in Miller's collections, and *Cordylodus angulatus* has not been reported from this section. Thus the *Iapetognathus* material occurs in essentially the same homotaxial position as *Ig. fluctivagus* in North America.

In summary, *Iapetognathus fluctivagus* occurs *in situ* in the *Iapetognathus* and *Cordylodus angulatus* Zones in the United States. In sections with detailed biostratigraphic control, occurrences in the *Cordylodus angulatus* Zone are only in the lower part of that zone. The species is known in slope deposits of apparently equivalent age in Kazakhstan, Nevada, and Canada.

Iapetognathus sprakersi

Iapetognathus sprakersi is younger than *Ig. fluctivagus* and has a much greater stratigraphic range. It occurs through 31.4 m of strata in the Lawson Cove section in Utah, from 57.0 m to 88.4 m above the base of the House Limestone (Fig. 1). The species occurs through all but the lowest part of the *Cordylodus angulatus* Zone and through the lower part of the very thick *Rossodus manitouensis* Zone. It occurs in comparable intervals of strata and in the same biozonal units in other sections of the House Limestone in Utah and Nevada (Table 4). Most other Nevada occurrences are also from the *C. angulatus* Zone or *R. manitouensis* Zone, with four exceptions. At USGS locations 11389-CO, 11400-CO, and 11404-CO in Nevada, *Ig. sprakersi* occurs in samples that may be from either the *Iapetognathus* Zone or the *C. angulatus* Zone. The fauna in these samples is insufficient to distinguish between these two possibilities. The fourth exception is the Vinini Formation material from Red Canyon in the Roberts Mountains (Table 4, location 24), which is redeposited limestone-pebble conglomerate in continental slope facies. The youngest conodonts in the conglomerate are earliest Whiterock in age (Ethington and others, 1995, p. 40).

Other occurrences of *Iapetognathus sprakersi* are the same age as the Utah occurrences. The material from Pennsylvania, Maryland, Virginia, Texas, Oklahoma, Colorado, and New Mexico (Table 4) is from either the *Cordylodus angulatus* Zone or the *Rossodus manitouensis* Zone. *Iapetognathus sprakersi* from New York is in the *R. manitouensis* Zone (Landing and others, 1996). Elements from Alaska are from the *C. angulatus* Zone. The age of the specimen from Yukon Territory is uncertain. The Russian material probably is from the *C. angulatus* Zone but may be as young as the *R. manitouensis* Zone. The Australian

material is from a sample that contains *Rossodus manitouensis* and can be correlated with the *R. manitouensis* Zone in North America.

The total range of *Iapetognathus sprakersi* is within the *Cordylodus angulatus* and *Rossodus manitouensis* zones. The species apparently begins slightly above the base of the former zone, and it is found only in the lower part of the latter zone in sections with continuous biostratigraphic data.

Iapetognathus aengensis

Iapetognathus aengensis occurs in one sample in the Lawson Cove section in Utah, 86.9 m above the base of the House Limestone and 1.5 m below the youngest occurrence of *Ig. sprakersi* (Fig. 1). This horizon is within the lower part of the thick interval of the *Rossodus manitouensis* Zone. The species also occurs in one sample in the same formation and zone in the nearby Drum Mountains, Utah (Table 1). Based on the ages of all occurrences of this species, the Utah material appears to be the youngest. The species is rare in Utah, but it is more abundant and has a longer stratigraphic range elsewhere.

The type material of *Iapetognathus aengensis* is from the Ceratopyge Limestone in Sweden (Lindström, 1955). Restudy of the formation by Löfgren (1996) indicates that its age is Arenigian, but the base of the formation contains redeposited conodonts of Tremadocian age, including *Ig. aengensis*. In Norway, Bruton and others (1988) reported specimens of *Iapetognathus* as *Ig. preaengensis* from the Naersnes section. The affinity of these specimens is ambiguous such that they can neither be confirmed or ruled out as specimens of *Iapetognathus*. Therefore, they do not contribute conclusively to discussion of the ranges of species of the genus, except to indicate that their occurrence there is in the lower part of the *Cordylodus angulatus* Zone. In Estonia (Table 1, locality 4), identification is uncertain for the lower of two occurrences of *Ig. aengensis* at the Tõnismägi Section (Kaljo and others, 1988). The upper occurrence of this species is associated with *Cordylodus angulatus*, indicating the *Cordylodus angulatus* Zone.

Occurrences of *Ig. aengensis* in Québec and New York are not associated with other taxa that are diagnostic of a particular biozone. Elements from the Broom Point South section in Newfoundland likewise are not associated with enough other index taxa to make a certain zonal assignment, and the sample containing these elements appears to have redeposited fauna. One illustrated element from the Woman Cove section in Newfoundland appears to be *Ig. aengensis*; it is from the *Cordylodus angulatus* Zone (Fåhræus and Roy, 1993).

Considering all occurrences, the oldest *Iapetognathus aengensis* specimens apparently occur at a slightly higher

stratigraphic level than the oldest *Iapetognathus fluctivagus*. The youngest *in situ* occurrence of *Ig. aengensis* appears to be at Lawson Cove, slightly below the youngest *Iapetognathus sprakersi* and in the lower part of the *Rossodus manitouensis* Zone (Fig. 1).

Iapetognathus jilinensis

Iapetognathus jilinensis occurs only at one location, in Jilin Province, China, where it ranges through less than one metre of strata. Ripperdan and others (1993) suggested that there is a hiatus or highly condensed interval approximately at that level in the section, so the range of this species may be short for that reason. It occurs with *Cordylodus lindstromi*, but it is overlain by an interval of about 12 m that has no conodonts diagnostic of a particular zone. *Cordylodus angulatus* occurs at the top of this interval (Chen and Gong, 1986), but Miller and Repetski found *Rossodus manitouensis* associated with the lowest *C. angulatus* in their collections from this part of the section. It appears that *Ig. jilinensis* in China may be approximately the same age as *Ig. fluctivagus* in the United States. Because of the short interval of strata in which it occurs, the complete range of *Ig. jilinensis* probably is not well established.

Iapetognathus landingi

Iapetognathus landingi occurs at only two locations. Most of our material is from three samples of one bed in the Manitou Formation in Colorado. *Ig. sprakersi* occurs in one of these samples. Associated conodonts are diagnostic of the *Rossodus manitouensis* Zone, but strata assigned to this zone are bounded by unconformities at the base and top. The Utah sample also is from the *R. manitouensis* Zone and also contains *Ig. sprakersi*. The stratigraphic position of this species within the *R. manitouensis* Zone illustrated on Figure 1 is unknown.

Iapetognathus spp.

Various other occurrences and reports of *Iapetognathus* species (see Table 5) are not identified herein to species, either because preservation is too poor or because the authors have not examined the mostly unillustrated material and thus are unable to determine species with confidence. The Utah sample (Table 5, locality 1) is from the *Cordylodus angulatus* Zone. The Alberta occurrence (Table 5, locality 2) is associated with trilobites and other conodonts that occur in the *Iapetognathus* Zone in the United States. The Argentina material (Table 5, locality 4) occurs slightly above the base of the *C. angulatus* Zone. The precise age of the Australian material (Table 5, locality 5) cannot be determined from the published faunal list. The age

of the Antarctic material (Table 5, locality 6) is undetermined because it comes from olistoliths in turbidites. The Estonian material (Table 5, locality 7) is coincident with the appearance of *Cordylodus rotundatus* and therefore correlates with the *C. angulatus* Zone. Although the species identifications are uncertain, the ages of all these occurrences are consistent with the known range of the genus.

REDEPOSITED OCCURRENCES OF *IAPETOGNATHUS*

Several of the occurrences of *Iapetognathus* species appear to be associated with conodont faunas that indicate stratigraphic admixture of faunas. In some cases this has meant that elements of *Iapetognathus* species have been mixed with younger species and in other cases older species appear to have been reworked to be associated with *Iapetognathus* species. Some of these occurrences are associated with continental slope environments and others with platform sediments.

An example of obvious redeposition of *Iapetognathus aengensis* into younger strata is in the Stora Backor locality in Sweden (Table 1, localities 1 and 2), from which this genus was first discovered (Lindström, 1955). *Iapetognathus* and *Cordylodus* are found in lowest Arenig strata on the Baltic Platform, but they are interpreted to have been redeposited as discrete elements after presumably having been eroded from Tremadocian strata (Löfgren, 1996). The setting of this reworking is on the shallowly dipping Baltic Platform succession where contemporaneous erosion and redeposition took place, perhaps repeatedly, in sea-level lowstands. The great majority of the reworked specimens show discoloration and abrasion relative to the better preserved Arenig specimens.

A second example of reworking is in the slope facies of the Green Point section in the Cow Head Group of Newfoundland. Strata in this section were deposited near the base of the continental slope (James and Stevens, 1986). Barnes (1988, Table 6) reported *Clavohamulus elongatus* Miller and *Hirsutodontus simplex* (Druce and Jones) associated with the lowest *Iapetognathus*, and he reported *Clavohamulus hintzei* Miller slightly lower. In other parts of North America, *Clavohamulus elongatus* occurs only in the upper part of the *Cordylodus proavus* Zone, three zones below the *Iapetognathus* Zone (Fig. 1). *Clavohamulus hintzei* and *Hirsutodontus simplex* occur in the *Cordylodus intermedius* Zone, two zones below the *Iapetognathus* Zone. It may be that the ranges of some of these taxa are longer in the colder deep water environment of the continental slope, but these stratigraphic associations could also be explained by downslope transport of conodonts from outcrops higher on the slope or adjacent platform.

Many occurrences of *Iapetognathus* in Tables 2 and 4 are from slope deposits in Nevada (Vinini and Valmy Formations). Some limestone samples that produced specimens of *Iapetognathus* in these strata are grainstones that were deposited as grain flows, and it is possible that conodonts in these samples were penecontemporaneously redeposited as discrete elements that originated on the adjacent carbonate platform or continental shelf edge. Such post-mortem lateral transport also requires caution in paleoenvironmental interpretations based on conodonts from these strata.

These examples caution us to examine the faunas under study for abnormal stratigraphic associations. Both situations can be easily accommodated, neither rule out stratigraphic utilization of the sections, but they do require that care is taken in assessing stratigraphic ranges of faunal elements.

ASSOCIATED TREMADOCIAN FOSSILS

An important aspect of the stratigraphic significance of *Iapetognathus* is its close association with graptolites and trilobites considered diagnostic of the base of the Tremadocian Series, the lowest series of the Ordovician System. The base of the Tremadocian Series was defined in North Wales at a point in rock that coincides with the lowest local occurrence of planktic graptolites (Rushton, 1982). In Norway, an *Iapetognathus* element identified as *Ig. aengensis* occurs about 2.5 m above the lowest planktic graptolite (Bruton and others, 1988). In Estonia the lowest occurrence of *Ig. aengensis* is slightly above the lowest planktic graptolites (Kaljo et al., 1988). The same conodont species occurs about one metre above the lowest planktic graptolite at the Broom Point South section in Newfoundland, Canada (Barnes, 1988). At the nearby Green Point section, *Ig. fluctivagus* occurs about three metres below the lowest planktic graptolites (Barnes, 1988). In New York, *Ig. aengensis* occurs about eight metres above early Tremadocian graptolites Landing, 1993). In New Mexico, *Ig. fluctivagus* occurs a few centimetres above a single occurrence of planktic graptolites (Taylor and Repetski, 1995). In China, the range of *Iapetognathus jilinensis* begins about 0.5 m above the lowest planktic graptolite (Nowlan and Nicoll, 1995). In Argentina, *Iapetognathus* sp. occurs about 10 m above the lowest planktic graptolites (Rao and Hünicken, 1995). Thus there is ample evidence that in several sections the lowest occurrences of *Iapetognathus aengensis*, *Ig. fluctivagus*, and *Ig. jilinensis* are closely associated with the base of the Tremadocian Series. *Iapetognathus sprakersi* is found in New Mexico above the planktic graptolites at the highest occurrence of *Ig. fluctivagus*.

Species of *Iapetognathus* are associated also with olenid trilobites that indicate an earliest Tremadocian age. In the Naersnes section in the Oslo area of Norway, the lowest planktic graptolite occurs about 2.5 m below the lowest certain occurrence of *Ig. aengensis* (Bruton and others, 1988), as noted above. This conodont occurs in a stink-stone concretion that contains the olenid *Jujuyaspis keideli norvegica*. Aceñolaza and Aceñolaza (1992) considered *Jujuyaspis* to be a good indicator of an earliest Tremadocian age. *Jujuyaspis* was named from Jujuy Province, Argentina, where Rao and Hünicken (1995) documented occurrences of *Iapetognathus* and *Jujuyaspis*. Their two samples that contain *Iapetognathus* sp. are ca. 30 m above *Jujuyaspis keideli keideli* in one of their two sections. As noted above, an unidentified species of *Iapetognathus* occurs about 10 m above the lowest planktic graptolites in this section.

Iapetognathus and *Jujuyaspis* occur together in several parts of North America, usually with other trilobites that are used for biozonation. In Texas, Stitt and Miller (1987) and Miller and Stitt (1995) reported that elements identified herein as *Iapetognathus fluctivagus* have a range that begins about 0.6 m below the lowest occurrences of the trilobites *Jujuyaspis borealis*, *Clelandia texana*, and *Symphysurina bulbosa*. Stitt and Miller (1987) also reported the same association in a bed in the lower part of the House Limestone in the Drum Mountains, Utah (Table 2). Miller and others (1990) and Miller and Taylor (1995) reported occurrences of several of these species in two other sections of the House Limestone in Utah. In the Chalk Knolls South section (Table 2) the lowest *Ig. fluctivagus* is in the same bed as *Jujuyaspis* sp. and *Clelandia utahensis*, and in Section A the range of *Ig. fluctivagus* begins 0.4 m below *J. borealis* and 0.7 m below *C. utahensis*. At the Lawson Cove section (Fig. 1), the lowest occurrences of *Iapetognathus fluctivagus* and *Iapetonudus ibexensis* are 0.6 m below a bed in which J.H. Stitt (personal communication to Miller) identified *Symphysurina bulbosa*? and 0.9 m below a bed in which he identified *Jujuyaspis borealis*. In New Mexico, *Ig. fluctivagus* occurs with *J. borealis* and *C. texana* less than one metre above early Tremadocian planktic graptolites (Taylor and Repetski, 1995).

In Alberta, Canada an unidentified species of *Iapetognathus* occurs with *Jujuyaspis borealis*, *Clelandia albertensis*, and *Symphysurina eugenia* (Westrop and others, 1981; Westrop, 1986). Based on the common association of *J. borealis* and *Clelandia* spp. with *Iapetognathus fluctivagus* in the United States, it is likely that the Alberta *Iapetognathus* is the species *Ig. fluctivagus*. However, we have not examined the specimens, so we include the Alberta material in Table 5 as *Iapetognathus* sp.

Miller and Stitt (1995) and Miller and Taylor (1995) noted the close association in North America of the lowest occurrences of *Iapetognathus* (herein referred to *Ig. fluctivagus*) with the lowest occurrences of the trilobites *Jujuyaspis borealis*, *Clelandia* spp., *Symphysurina bulbosa*, and other species of *Symphysurina*. It appears that the base of the *Iapetognathus* Conodont Biozone is essentially at the same stratigraphic level as the base of the *Symphysurina bulbosa* Trilobite Biosubzone of the *Symphysurina* Trilobite Biozone. Where the bases of the zones are not coincident, the conodont zone may begin as much as one metre stratigraphically below the trilobite zone. Thus there is a close relationship between the lowest occurrences of the conodonts *Iapetognathus fluctivagus*, *Iapetonudus ibexensis*, and trilobite species assigned to three families: Olenidae (*Jujuyaspis*), Kingstonidae (*Clelandia*), and Nileidae (*Symphysurina*). Other conodont taxa not considered in this report also have lowest occurrences in the narrow stratigraphic interval where these other faunal elements first appear. Planktic graptolite taxa appear at what seems to be essentially the same level in other parts of the world. The diversity of new fauna that appeared at approximately the same time makes this stratigraphic level attractive as the boundary horizon for the base of the Ordovician System.

In summary, the lowest occurrences of *Iapetonudus ibexensis*, *Iapetognathus aengensis*, *Iapetognathus fluctivagus*, *Iapetognathus jilinensis*, and (in Argentina) *Iapetognathus* sp. are all closely associated with occurrences of planktic graptolites and several species of trilobites (especially the olenid *Jujuyaspis*) that are considered to indicate an earliest Tremadocian age. Based on current data, the earliest occurrences of these four species of *Iapetonudus* and *Iapetognathus* are close to one another. Specimens of *In. ibexensis* and *Ig. fluctivagus* occur earliest in many sections and the earliest specimens of *Ig. aengensis* seem to appear in consistently younger strata. From stratigraphic distributions it is clear also that *Iapetognathus sprakersi* appeared somewhat later than *Ig. aengensis*, *Ig. fluctivagus*, and *Ig. jilinensis*. In addition, the two known occurrences of *Iapetognathus landingi* are significantly younger than the lowest occurrences of all other species of the genus. Further study will be needed to refine the relationships among their earliest appearances.

DIFFERENTIATION OF IAPETONUDUS, IAPETOGNATHUS AND THEIR SPECIES

Differentiation of the five named species of *Iapetognathus* (*Ig. aengensis*, *Ig. fluctivagus*, *Ig. jilinensis*, *Ig. landingi* and *Ig. sprakersi*) and the single species of *Iapetonudus* (*In. ibexensis*) is made primarily on the presence or absence of lateral processes. All elements of all species of

Iapetognathus have at least one, or sometimes two, lateral processes, and the process usually supports one or more discrete denticles. Elements of *Iapetonudus* lack developed lateral processes, but some elements may have a carina on the inner or both inner and outer lateral margins.

Species of *Iapetognathus* are differentiated using a number of characteristics, including the location of lateral processes, the number of denticles developed on the lateral process, the direction of compression of the cusp and its cross-sectional shape, and the height of the connection at the junction of the cusp with the lateral process. Details are provided in the taxonomic section.

ORIGIN, EVOLUTION AND SPECIATION OF IAPETOGNATHUS

Based on the overlap of stratigraphic range and several examples of close morphologic similarity, *Iapetognathus* is thought to have developed from the modified coniform-coniform apparatus of *Iapetonudus ibexensis* with the development of true processes and denticulation from one or both of the carinae (proto-processes). The essential morphology of the cusp of both *Iapetonudus ibexensis* and *Iapetognathus fluctivagus* are indistinguishable. Also, the processes develop from the positions of the proto-processes.

Iapetognathus jilinensis may have evolved from *Ig. fluctivagus* or they may have been geographically isolated species because they have not been found together or in stratigraphic succession. *Iapetognathus sprakersi* most likely is derived from *Ig. fluctivagus* with lateral thinning of the cusp and a reduction of the height of the bar of the lateral process. These two species are similar and juvenile specimens of *Ig. fluctivagus* can be mistaken for elements of *Ig. sprakersi*.

Development of *Iapetognathus aengensis* could have been either directly from *Ig. fluctivagus* or through either *Ig. sprakersi* or *Ig. jilinensis*. In either case there must have been a progressive reduction in the posteriorly directed outer-lateral process and development of an anterior process that is inner-lateral in position.

Iapetognathus landingi appears to be the youngest species of the genus thus far recognized. It is similar to *Ig. aengensis* and probably evolved from that species with the development of striae on the cusp and denticles and with the development of a large costa on the inner side of the cusp.

TAXONOMY

Understanding of the taxonomy and apparatus structure of *Iapetognathus* and *Iapetonudus* has been hampered by the paucity of elements of species of these genera. The degree of morphologic diversity and the lack of similarity to other ramiform genera of similar age, such as

Cordylodus, has further compounded the problem. A sample from the Lawson Cove section, Utah and a sample from the Ceratopyge Limestone from Stora Backor, Sweden have been critical in supplying enough specimens to decipher the morphology of the genus. The large sample from 438 ft. in the Lawson Cove section has yielded 500 elements of *Iapetognathus fluctivagus* and more than 10,000 other conodont elements. None of the coniform or ramiform elements found in the sample appear to be possible symmetrical elements which could be associated morphologically with *Iapetognathus fluctivagus*. All of the symmetrical coniform elements have been associated with other coniform apparatuses and the symmetrical ramiform elements are all associated with species of *Cordylodus*. This lack of a symmetrical (Sa) element may make this lineage unique among conodonts, because the authors know of no other multielement ramiform genus lacking an Sa element.

Lindström (1955) and Landing *in* Fortey and others (1982) both indicated that the apparatus of *Iapetognathus* (*Pravognathus*) was monoelemental, but Lindström's original illustration of the genus included three element types. Barnes (1988) illustrated a septimembrate apparatus, but did not describe the individual elements. Some of the elements illustrated by Barnes (1988, Fig. 13, y, bb, dd, ee) probably are not part of the apparatus of *Iapetognathus*, but the quality of reproduction of the plate is too poor to assess this apparatus fully.

Landing *in* Landing and others (1996) described a new species, *Iapetognathus sprakersi*, with minimal diagnosis and description. His species, based on only 10 elements, apparently was considered to be monoelemental, following his definition of the genus (Landing, *in* Fortey and others, 1982). With the more than thirty elements available in this study, and using the *Ig. fluctivagus* model, we have been able to recognize only three element types in the apparatus of *Ig. sprakersi* which conform to some of the morphologies expressed in *Ig. fluctivagus*.

In terms of element structure and apparatus element configuration, the majority of ramiform-ramiform and ramiform-pectiniform apparatuses are composed of elements which have a posterior process. However, elements with only lateral processes like those of *Iapetognathus*, which are assumed to be oriented transverse to the axial plane of a linear apparatus, are relatively common in taxa of Ordovician and Silurian age. Examples include the P elements of *Erraticodon* (Nicoll, 1995), some of the S elements of *Oulodus*, *Plectodina*, and several other common genera (e.g. Sweet, 1988). *Iapetognathus* thus appears to be just an early example of transverse element configuration in conodont apparatus structure.

In the septimembrate apparatus structure that we have been able to recognize in some species of *Iapetognathus*,

we are able to apply the Sweet (1988) M-S-P element notational scheme to most of the elements. These include Sc, Sb and Sd recognized for their increasing degree of asymmetrical complexity, and Pb–Pa based on the presence of two similar but distinct element types. However, we are unable to classify two of the element types of the *Iapetognathus* apparatus in the M-S-P scheme. Neither element is symmetrical and neither conforms well with the general morphology that Nicoll (1977) has suggested should delineate an M element—the presence of a buttress on a transversely oriented element with a large tine-like cusp. For this reason, we are using the element notations Xa and Xb for these elements until we are able to place them in a more conventional apparatus notational scheme. These terms are not meant to be regarded as permanent element designations, but as temporary tools allowing us to easily describe components of these apparatuses.

PRESERVATION OF MATERIAL STUDIED

Much of the material studied for this investigation is less than ideally preserved. Specimens from the Lawson Cove section in particular, and the western Utah region generally, have CAI 4 values, or sometimes higher, and also they are consistently overgrown with post-depositional apatite that prevents observation of some features on many specimens. Material from the Lange Ranch section in Texas has a low alteration value (CAI 1–1.5) but most of the specimens also have apatite overgrowth that obscures some surface morphology. Material from the Dayangcha XCS section in Jilin has a CAI value of 3 and suffers from encrusting fine quartz sand or silt grains and glauconite pellets, as well as some apatite overgrowth. Material from eastern North America, with the notable exception of parts of western Newfoundland, usually has elevated CAI values. Material from Stora Backor in Sweden has a low CAI value of 1.5, but appears to be slightly rounded by post-depositional abrasion and polishing.

Despite these problems, the preservation of specimens from all localities is adequate to allow examination of all of the necessary morphologic features needed to both define the species and to understand the morphological evolution involved.

REPOSITORY OF SPECIMENS

Illustrated specimens are stored in the United States National Museum, Washington, D.C., U.S.A.

Genus IAPETOGNATHUS Landing, 1982

Type species. Pravognathus aengensis Lindström 1955

Diagnosis. Septimembrate apparatus of S (Sc, Sb, Sd), P (Pb, Pa) and X (Xa, Xb) elements. All elements ramiform,

with a large posteriorly recurved or inclined cusp and one or two denticulate processes. The major process is laterally directed, either as a posteriorly directed outer-lateral process or as an inwardly directed antero-lateral process. The X elements appear to have the cusp recurved over one of the processes, which may be in a posterior direction. No symmetrical (Sa) or makelliform (M) elements have thus far been associated with the apparatus, but Sc, Sb, Sd, Xa, Xb, Pb and Pa elements have been differentiated in one or more species. The cusp of most elements of this genus may have one or more well developed keels or carinae, usually anteriorly or laterally located, that terminate abruptly well above the basal margin of the element. The cusp may be either laterally or antero-posteriorly compressed. Most species are characterized by elements with smooth surfaces, but some have costae and one species has well developed striae.

All species of *Iapetognathus* are characterized by elements with a prominent cusp that is erect at the base but tends to become recurved posteriorly above the level of the lateral or anterior process. In the S and P elements the cusp usually is curved posteriorly and out of the plane of any of the processes, but in the X elements the cusp is recurved over a posteriorly directed process. In *Ig. aengensis*, there is a denticulate posterior process in the Pa and Pb elements.

Remarks. *Iapetognathus* was established by Landing (in Fortey & others, 1982) as a monoelemental genus based on *Pravognathus aengensis* Lindström (1955), and a new species, *Ig. preaengensis* Landing was described in the same paper. We concur with Landing that the generic assignment, to *Pravognathus* Stauffer (1936), made by Lindström (1955) for his material from Stora Backor was incorrect. Examination of specimens of *Pravognathus idonea* (Stauffer) from the Platteville Formation from Minnesota indicate that this genus lacks a distinct basal cavity extending into the cusp and has only a broad excavation under the central part of the element. *Iapetognathus* has a basal cavity that extends upward into the cusp to about one quarter of its height, and this distinguishes the genus from *Pravognathus*.

In our re-examination of topotype material from Stora Backor, we have been able to define a multimembrate apparatus for *Ig. aengensis* that includes elements identical with the material assigned to *Ig. preaengensis* by Landing in Fortey and others (1982). We thus conclude that *Ig. preaengensis* Landing is representative of the Sc elements that we recognize in the apparatus of *Ig. aengensis* and accordingly place the two species in synonymy.

Barnes (1988, Fig. 13, y-ee) illustrated a septimembrate apparatus that he ascribed to *Ig. preaengensis*, but he did not describe the elements; the illustrations are not

adequate to establish either the morphology or identification of the elements with certainty. Although one of the authors [GSN] has had the opportunity to examine the oldest material referable to *Iapetognathus* from western Newfoundland, none of us has seen specimens from the level of the illustrated material. Some of the elements illustrated are probably assignable to *Iapetognathus fluctivagus* (Barnes, 1988, Fig. 13z, aa) and to *Ig. aengensis* (Barnes, 1988, Fig. 13cc) whereas others are probably parts of a *Cordylodus* apparatus (Barnes, 1988, Fig. 13y, bb, dd, ee).

Iapetognathus may be distinguished from *Cordylodus* and *Eodontatus* by the symmetry of the elements, especially the S elements of *Iapetognathus* which lack of a denticulate posterior process developed in the plane of the posteriorly recurved cusp.

IAPETOGNATHUS AENGENSIS (Lindström)

Pl. 1, Figs. 1a-5f; Pl. 2, Figs. 1a-4g; Pl. 3, Figs. 1a-4e; Pl. 4, Figs. 1a-3f, Pl. 5, Figs. 1a-3f

v. *Pravognathus aengensis* LINDSTRÖM, 1955, p. 585, Pl. 5, figs. 10-13 (Fig. 10 = Sd element, Fig. 11 = Sc element, Figs. 12, 13 = Sb element).

v. *Iapetognathus preaengensis* LANDING, 1982, in FORTEY, LANDING, and SKEVINGTON, p. 124-126, Text-figs. 6 (B, C), 8 (B, C, H)(8B, 8C & 8H = Sc elements); v. LANDING, BARNES, and STEVENS, 1986, p. 1934, Pl. 1, fig. 8; v. (non?) BRUTON, KOCH, and REPETSKI, 1988, p. 454, Fig. 4 (a, b); v. BARNES, 1988, Fig. 13cc only (non Fig. 13y, z, aa, bb, dd, ee); KALJO AND OTHERS, 1988, Figs. 4f, 5f.

Iapetognathus sp. KALJO AND OTHERS, 1986, Pl. 3, fig. 13; KALJO AND OTHERS, 1988, Figs. 4bb, 5bb only.

Iapetognathus aengensis (LINDSTRÖM). OLGUN, 1987, p. 60, Fig. 30; LOFGREN, 1996, p. 173, Fig. 8(G, K).

Iapetognathus preaengensis [sic] LANDING. LANDING, 1993, p. 11, Fig. 8-1, (?Fig. 8-2).

Iapetognathus sp. aff. *I. preaengensis* LANDING. FÄHRÆUS & ROY, 1993, Pl. 2, fig 26, (=Sc or Sb element), not Figs 25, 27 (= *Cordylodus* sp.).

Material studied. 138 elements.

Diagnosis. Multimembrate apparatus in which six element types have been identified. All elements ramiform with a large inwardly directed anterior process supporting up to four denticles. Posterior process reduced or absent, except for the P elements. Cusp large, laterally compressed, and erect to posteriorly inclined and bent inward. Albid tissue in cusp and denticles, base mostly hyaline. Basal cavity deeply excavated under the cusp of all elements

and extending under the processes. Lacks Sa and M elements, but has elements assigned to Sc, Sb, Sd, Xb, Pb and Pa positions.

Description. Apparatus probably septimembrate in which only six elements, Sc, Sb, Sd, Xb, Pb and Pa, are recognized. All elements are ramiform with a large anterior process and, with the exception of the Pa element, a short posterior process. The anterior process supports up to four denticles that are laterally compressed in the plane of the process and the two distal denticles tend to be splayed away from the cusp. The cusp is laterally compressed. The surface of all elements is smooth, lacking striae, but some elements may have short costae. Albid tissue is confined to the cusp and denticles, and the thin-walled base is hyaline.

The Sc element (Plate 1) has a large erect to posteriorly recurved cusp that has a biconvex cross-section with keels. The keel of the posterior margin of the cusp becomes less well defined toward the base and usually does not extend to the basal margin. An anterior inner-lateral process supports four or five discrete denticles. The denticles are laterally compressed in the plane of the process and tend to be curved slightly inward. There is no posterior process, but there is a bluntly rounded posterior shelf that may support one or two short carinae on the outer-lateral margin that could possibly represent a vestigial posterior process. The base is deeply excavated under the cusp and extends, without constriction, under the long anterior process and the short rounded posterior shelf.

The Sb element (Plate 2) is similar to the Sc element except for the posterior margin. The prominent keel of the posterior margin of the cusp is drawn out to form a short crest linking the cusp to a point near the posterior tip of the element. In plan view the element tip is tapered rather than rounded as in the Sc element. This posterior end of the element is bowed upward. In some forms the posterior keel of the cusp has the appearance of a narrow adentate ridge. The anterior inner-lateral process supports three or four laterally compressed denticles, the anterior-most of which incline forward relative to those proximal to the cusp. In some elements the denticles are partly fused near their bases, but are discrete near their tips. As in the Sc element, the base of the Sb element is deeply excavated under the cusp and this extends, without constriction, under the anterior inner-lateral process and short posterior extension. However, unlike the Sc element, but somewhat more like the Sd element, the anterior inner lateral process of the Sb element may be narrowed slightly just anterior to the cusp and before the proximal denticle. Like the Sd element, the Sb element is commonly broken at this point.

The Sd element (Plate 3) differs from the Sc and Sb elements in having both the anterior inner-lateral process

and the short adentate posterior process narrow abruptly from the width of the basal part of the cusp. The anterior inner-lateral process supports at least four denticles and the posterior extension is adentate, as in the other S elements. The proximal denticle of the process appears to be slightly larger than the rest of the process denticles and the process tends to narrow between the proximal denticle and cusp. A large number (17 of 37) of the Sd elements in our collections have the anterior process broken off and only the cusp and posterior margin are preserved. The outer margin is bent inward at the base giving the element a flexed appearance. The process denticles are similar to those found on the Sc and Sb elements. The cusp is biconvex in cross-section and bent inward. The base is deeply excavated under the cusp, but is sharply narrowed under the anterior inner-lateral process and also tapers abruptly under the posterior extension.

Only a single X element has been recovered and on the basis of the lack of denticles on the posterior process it is assigned as the Xb element (Pl. 4, fig. 1a-f). The cusp is broken in this element, but it appears to have been reclined or recurved in the plane of a short, broadly rounded and adentate posterior process. The anterior inner-lateral process is relatively long, and supports four denticles that are slightly compressed in the plane of the process. The plane of the process axis is almost at right angles with the plane of the cusp. The base of the element is partly broken, but it appears to be broadly excavated under the cusp and processes.

A total of only five P elements have been recovered Pl. 4, figs. 2, 3; Pl. 5, figs. 1-3) including three left Pb elements and one right and one left Pa elements. The Pb elements are elongate, straight to bowed slightly outward with an inwardly bent, but essentially erect cusp. There are at least four laterally compressed denticles on the long anterior process and a single denticle on the posterior process. The denticles of the anterior process tend to incline forward, away from the cusp, as well as being slightly curved inward. A keel extends along the length of the process and denticle margins and all denticles and the cusp are biconvex in cross-section. In plan view the element is widest at the cusp and tapers to both posterior and anterior tips. The base is most deeply excavated under the cusp, and a trough narrows slightly as it extends under both anterior and posterior processes.

The Pa element has a cusp and two processes of sub-equal length, one posterior and one anterior that are inwardly bent. Each process supports two denticles. The cusp and denticles are all discrete and laterally compressed in the plane of the process. The cusp is an integral part of the posterior process. Like the Pb element, the denticles of the anterior process are angled slightly forward, away from the erect or slightly reclined cusp. The base of the

element is excavated under the cusp and a trough extends under both anterior and posterior processes.

Remarks. Analysis of this species had been difficult because it is morphologically rather dissimilar from other species of the genus, and material for study was limited. We have oriented the elements on the basis of the shape and curvature of the cusp and the location and character of the basal cavity, especially the cavity tip. Unlike most species of *Iapetognathus*, *Ig. aengensis* has the major process directed anteriorly. However, the profile view of the cusp (Plate 1, Fig. 4f) is essentially the same as for that of *Ig. fluctivagus* or *In. ibexensis*. Despite these morphologic differences, *Ig. aengensis* is typical of species of *Iapetognathus* because it lacks a symmetrical (Sa) element and an M element. The single X element recovered has a morphology similar to the X elements of *Ig. fluctivagus*.

Lindström (1955) illustrated (Pl. 5, figs. 10–12) all three of the elements of *Pravognathus aengensis* recovered in his study. Examination of those elements suggests that they represent Sd (Fig. 10), Sc (Fig. 11) and Sb (Fig. 12) element types. These three element types were also the most common in our re-sampling of the Stora Backor interval that produced Lindström's material.

The recovery of *Ig. aengensis* in the Lawson Cove, Naersnes and Green Point sections establishes the presumed correct stratigraphic position of the species, rather than the reworked material from the Stora Backor locality. However, it is the abundance of material from the Swedish locality that has allowed reconstruction of the apparatus structure.

Geographic distribution. The distribution of *Ig. aengensis* has been discussed earlier herein. See also Table 1 for a summary of its known distribution.

Stratigraphic range. *Iapetognathus aengensis* appears to have the longest range of any of the species of the genus, from a level within the *Iapetognathus* Zone near the base of the Tremadocian to the lower part of the middle Tremadocian *Rossodus manitouensis* Zone (Fig. 1). Its oldest known appearances are in the Cow Head Group, western Newfoundland and in the Alum Shale Formation near Oslo, Norway. At the Green Point section, Newfoundland (Barnes, 1988), the species first appears in the middle to upper part of Bed 25 (of James and Stevens, 1986). This level is considerably below the level of appearance of Assemblage 2 graptolites and of *Cordylodus angulatus*. At the Naersnes section, Norway (Bruton et al., 1988), *Ig. aengensis* appears in a calcareous concretion also containing the trilobite *Jujuyaspis keideli norvegicus*, and about 20–25 cm above the lowest occurrence of Assemblage 2 graptolites, here marked by *Rhabdinopora flabelliformis flabelliformis*. (As mentioned earlier, we now consider as doubtful the identification of the two specimens at Naersnes attributed to *Ig. preaengensis* [= *aengensis*] by

Bruton and others (1988) that occur with Assemblage I graptolites and with the earliest Tremadocian trilobite *Boekaspis hirsuta*.) Additionally, Landing (1993) reported *Ig. praeangensis* [sic] (herein synonymized under *Ig. aengensis*) from the Hatch Hill Formation in eastern New York, at a level above, and perhaps arguably within the range of, *Rhabdinopora flabelliformis rustica* (Bulman). As mentioned by Landing (1993, p. 10), *Rh. f. rustica* appears below the lowest *Anisograptus*, which is taken as the first of the Assemblage 2 taxa locally in western Newfoundland; thus, this New York occurrence could well be another occurrence of *Ig. aengensis* within the upper part of the range of graptolite Assemblage 1.

Iapetognathus aengensis ranges upward into the middle Tremadocian. Rao and Hünicken (1995) reported *Ig. preaengensis* from the lower part of the Cardonal Formation at their Amarilla Creek section in Jujuy Province, northwestern Argentina. If these unillustrated specimens are indeed *Ig. aengensis*, then it occurs there in the lower part of the *Cordylodus angulatus* Zone, appearing at a level nearly 30 m above the appearance of the trilobite *Jujuyaspis keideli keideli* and within an interval beginning approximately 12 m above an occurrence of Assemblage I graptolites and about 7 m below middle Tremadocian Assemblage 3 graptolites and trilobites of the *Kainella meridionalis* Zone. A somewhat younger occurrence of *Iapetognathus aengensis* is at the Lawson Cove section, Utah, where it has been found at a level low in the *Rossodus manitouensis* Zone. We consider the occurrences of *Ig. aengensis* in the overlying biozones in southern and central Sweden (e.g., at Stora Backor) (Lindström, 1955; Ölgun, 1987) to be due to reworking (see also Löfgren, 1996).

IAPETOGNATHUS FLUCTIVAGUS new species

Pl. 6, Figs. 1a–5d; Pl. 7, Figs. 1a–4g; Pl. 8, Figs. 1a–2g; Pl. 9, Figs. 1a–7f; Pl. 10, Figs. 1a–6g; Pl. 11, Figs. 1a–6h

- v. *Iapetognathus* n. sp. TAYLOR and REPETSKI, 1995, p. 135.
- v. *Iapetognathus* n. sp. 1 MILLER and STITT, 1995 p. 108; v. MILLER and TAYLOR, 1995, p. 111.
- v. New Genus A MILLER, 1970, p. 110, Pl. 1, figs. 32–34; Text-fig. 11E.
- v. New Genus 2 (cordylodid) MILLER AND OTHERS, 1982, Text-figures 5, 6.
- v. *Iapetognathus preaengensis* Landing. MILLER, 1987, Fig. 3; BARNES, 1988, Fig. 13z, aa, non Fig. 13cc (= *Ig. aengensis*), Fig. 13bb, dd, ee (= *Cordylodus* sp.).

Material studied. More than 500 elements.

Etymology. From the Latin *fluctus*- a wave, and *vagare* to wander; wandering over the waves—a reference to the wide distribution of the species.

Diagnosis. A septimembrate ramiform-ramiform apparatus of P (Pb, Pa), S (Sc, Sb, Sd) and X (Xa, Xb) elements. The cusp of all elements of *Ig. fluctivagus* is laterally compressed and bent posteriorly. The major denticulate process is in an outer lateral position. Denticles may be present on a second process that is inwardly or posteriorly directed. The processes are strongly attached to the cusp, and the outer-lateral process usually supports two denticles in the Sc, Sb and Sd elements. The base of the element is deeply excavated, extending without constriction under the processes, and the cavity tip extends into the base of the cusp. Albid tissue is confined to the upper part of the cusp and denticles. The surface of the elements is smooth, lacking striae.

Description. Multimembrate apparatus, in which seven elements (Sc, Sb, Sd, Pb, Pa, Xa and Xb) are differentiated in the material studied. The cusp of all element types is strongly compressed laterally and recurved posteriorly. The processes are directed laterally or postero-laterally, with a posteriorly directed process present only in what we have called the Xa and Xb elements. The Sd element may have denticles on both inner and outer processes, the Xa and Xb elements also have denticles on both processes, but other S and P elements have denticles only on the outer process. The surface of the elements is smooth, with no striae or costae.

The laterally compressed cusp of all elements has a prominent keel on the anterior margin that terminates abruptly proximally, usually a little above the level of the upper surface of the adjacent lateral process. Many elements have a distinct node about half way between the keel and the basal margin located along the projected line of the cusp keel. Most elements have a second keel on the posterior cusp margin, and some may have a third, but less well developed, lateral keel. Denticles of the processes are compressed in the plane of the process and have sharp keels. The keel from the proximal denticle of the process usually does not extend up the lateral face of the cusp, but ends low on the cusp. Only three elements, two Sc and one Sb, of the more than 450 elements recovered from the Lawson Cove 438 ft. sample have more than two denticles on the lateral process.

On S elements the anterior basal margin curves smoothly to the posteriorly directed outer lateral process. This gives the appearance of the process attaching smoothly with the anterior edge of the cusp. However, the axial plane of the process, as defined by the denticles, intersects the midpoint of the cusp. The outer lateral process usually supports two denticles and the inner lateral process, if present, has only a single denticle.

The Sc element has a broadly rounded inner lateral margin either lacking or with a reduced posterior keel on the lower part of the cusp. The outer-lateral process supports one or two denticles that are compressed parallel to the axial plane of the process, and there is a well developed keel along the crest of the process and denticles. The denticles are erect or may be slightly inclined posteriorly, but they are not posteriorly recurved like the cusp. The inner lateral margin of the element flares downward and is broadly rounded.

The Sb element has an outer lateral process similar to that found on the Sc element, but there is a well developed keel on the posterior margin of the cusp that twists outward to extend down the posterior edge of the base. This keel differentiates the Sc and Sb elements.

The Sd element is similar to the Sb element except for the presence of denticles on both the inner and outer lateral processes. The inner lateral process denticle develops on the crest of the process, in approximately the same position as the keel of the Sb element.

The X elements have a broadly rounded anterior margin and denticles on one or both processes. In oral view the angle formed between the axial line of the processes approximates a right angle. The cusp is located at the junction of the processes, and the upper part of the cusp is twisted to align with the posterior process. The other process is considered to be an outer lateral process. The cusp is laterally compressed and appears to be bent back over the posterior process. The Xa element has at least one large denticle on the posterior process and one or two denticles on the outer lateral process. The Xb element may have a well developed keel or a small laterally compressed denticle along the crest of the posterior process and one or two denticles on the outer lateral process. The inner lateral margin of the cusp is very steep, unlike the strongly flared margin of the S elements.

The P and S elements are differentiated by the apparent relationship of the outer lateral process to the cusp and the shape of the inner lateral margin. In plan view of both P and S elements the axial line of the process intersects the midline of the outer side of the laterally compressed cusp. In the S and M elements the anterior basal margin sweeps broadly around from the cusp to the process, but in the P elements this margin extends back from the cusp at an angle of about 45 degrees until it bends outward to follow the axial line of the process. This gives the appearance in P elements that the anterior margin of the cusp is thrust forward from the process. The inner lateral margin of the cusp is steeper in P elements than in S elements, and the basal margin is less strongly flared inwardly. In this character, the P and S elements are generally similar.

The Pa element has the laterally compressed cusp twisted so that the angle formed between the plane of the long axis of the cusp and the plane of the axis of the outer lateral process is less than 45 degrees. The outer lateral process usually supports two denticles, and there is no inner lateral process. The inner lateral face of the element is slightly rounded and not strongly flared.

The Pb element is similar to the Pa element except the long axis of the cusp is essentially at a right angle to the axis of the process. Thus, the cusp orientation of the Pb element is similar to that of S elements. The outer lateral process usually has two denticles, and there is no inner lateral process.

Albid tissue. Distribution of albid tissue in *Ig. fluctivagus* is usually restricted to the cusp and denticles. The transition from the hyaline tissue of the crown base to the albid tissue is abrupt and planar in both cusp and denticles. A few specimens have a little albid tissue present along the oral margin linking the albid tissue of adjacent denticles, but not between process denticles and the cusp. There also may be some diffuse albid tissue scattered about the base of the crown.

Basal cavity and attachment cone. All elements have a large, open basal cavity that is present, undifferentiated, under cusp and processes. The cavity tip is located against the anterior margin of the element and extends upward to near the level of the albid tissue of the cusp. The attachment cone of material from both Utah and Texas is poorly preserved or, more frequently, absent. When present, the attachment cone appears to be similar to that found in *Ig. jilinensis*, and is thin, extending outward following and extending the apron of the crown.

Remarks. Due to the curved geometry of the cusp and processes the orientation of specimens is difficult and only slight differences in orientation exaggerate both differences and similarities in element morphology.

Iapetognathus fluctivagus is differentiated from *Ig. sprakersi* by its strong attachment of the outer-lateral process to the cusp. It is differentiated from *Iapetonudus ibexensis* by the development of denticulation and distinct lateral processes. *Ig. fluctivagus* is most similar to *Ig. jilinensis*, but differs in having a strongly laterally compressed cusp and fewer denticles on the outer lateral process.

Geographic distribution. *Iapetognathus fluctivagus* is widespread in North America and occurs in the United States in Nevada, Utah, Colorado, New Mexico, Texas and Oklahoma; it also occurs in Newfoundland, Canada. Outside of North America, it has been found only in Kazakhstan. Details of its geographic occurrence, as well as literature references, are presented in Table 2, and its occurrence was discussed more fully in a previous part of this report.

Stratigraphic range. The lowest occurrence of *Iapetognathus fluctivagus* characterizes the base of the *Iapetognathus* Zone in North America. In the Lawson Cove section in the Wah Wah Mountains, Millard County, Utah (Table 2, locality 7), this species occurs through 6.1 m of strata in the lower part of the House Limestone. This interval constitutes the *Iapetognathus* Zone and the lowermost part of the *Cordylodus angulatus* Zone, as shown in Fig. 1. The range of this species is quite short, but it is common within this range and occurs in 14 of 15 samples collected through its total range in the Lawson Cove section. Overlying samples contain elements assignable to *Ig. sprakersi*. *Ig. fluctivagus* is known from the same biostratigraphic interval elsewhere in North America (Table 2).

IAPETOGNATHUS JILINENSIS new species

Pl. 12, Figs. 1a–4f; Pl. 13, Figs. 1a–3f;
Pl. 14, Figs. 1a–4b

v. *Iapetognathus* n. sp. A NOWLAN and NICOLL, 1995, p. 115–116.

Material studied. 45 elements.

Etymology. For the Province of Jilin, north-east China, where the species was first recognized.

Diagnosis. Probable septimembrate apparatus of which only six element types are recognized. These include the Sc, Sb, Sd, Xa, Pa and Pb elements. All elements have a denticulate outer-lateral process; the Xa element also has a posterior process. The outer-lateral process supports two to four denticles. The cusp and denticles are antero-posteriorly compressed.

Description. The Sc element has a posteriorly bent cusp that is antero-posteriorly compressed and has keels on the inner and outer lateral margins. The outer keel line continues into the keel line of the antero-posteriorly compressed denticles of the outer-lateral process. The inner margin keel terminates abruptly on the margin of the cusp at about the level of the base of the V that is formed between the cusp and the first denticle of the outer-lateral process. The outer-lateral process supports three or four denticles that are discrete and splayed outward, away from the cusp. The process is relatively low and narrow. The basal inner lateral margin of the element is directed downward, extending below the basal margin of the process.

The Sb element is similar to the Sc element, except for a third keel or costa, that develops low on the posterior margin of the cusp. From a point slightly above the base of the V that is formed between the cusp and the first process denticle, a costa develops on the posterior margin of the cusp and extends down to the basal margin of the element. As in the Sc element, the keel or costa on the

inner lateral edge of the cusp terminates abruptly at about the level of the V formed at the junction of the cusp and the lateral process.

A single broken element is designated as an Sd element. The element appears to have been of similar shape to the Sc and Sb elements, except for the presence of four ribs, or keels on the cusp (Pl. 13, Fig. 2c). The cusp is ovate and antero-posteriorly compressed with a keel leading to the denticle line of the outer-lateral process. There is a second keel on the posterior face of the cusp and this extends down onto the basal flange. The third keel is located on the inner margin of the cusp and the fourth is located on the anterior margin, but closer to the inner than the outer margin. In the only element assigned to this element type, the outer lateral process is broken at the outer edge of a single ovate, antero-posteriorly compressed cusp.

The Xa element has two denticulated processes. A short posterior process has a single denticle and a longer outer-lateral process has four denticles. The cusp is sub-round in cross-section with a keel extending to both processes. The denticles of the outer-lateral process are anterior-posteriorly compressed, and the denticle of the posterior process is laterally compressed. The cusp is broken so that it is not clear if it is erect or bent over the posterior process. The inner basal margin of the element is rounded smoothly into the basal anterior margin, as is the case with the S elements. The attachment cone is partly broken and the inner surface partly obscured with debris.

The P elements are similar to the S elements but differ in having a more compressed cusp cross-section. The Pa element has an antero-posteriorly compressed cusp with two keels. The outer lateral process supports at least two antero-posteriorly compressed denticles. The cusp appears slightly twisted, so that a plane drawn through the two keels will pass behind the plane of the outer-lateral process. The Pb element is similar to the Pa element except for the cusp which is not twisted but has the axial plane drawn between the two keels aligned with the outer-lateral process. Unlike the P elements of *Ig. fluctivagus*, the anterior margin of the cusp of the P elements does not appear to protrude forward.

Remarks. *Iapetognathus jilinensis* differs from other species of the genus in having the cusp compressed in an anterior-posterior direction. Like both *Ig. fluctivagus* and *Ig. sprakersi*, the major process is developed in an outer lateral position. The outer lateral process carries more denticles, usually 3 or 4, than found in these species as well. The distribution of albid and hyaline tissues is similar to that found in *Ig. fluctivagus*.

Geographic distribution. *Iapetognathus jilinensis* has been found only in the topotype locality, the Xiaoyangxiao Critical Section (XCS), near Dayangcha, Jilin Province,

China (Nowlan and Nicoll, 1995). The species is present in the original Chinese collections (Chen and Gong, 1986; Duan, An and Zhao, 1986) and in subsequent collections made to evaluate the Cambro-Ordovician boundary interval at that locality.

Stratigraphic range. *Iapetognathus jilinensis* occurs about 0.8 m above the first occurrence of the graptolites including *Rhabdinopora proparabola* and *R. flabelliformis* (Chen and others, 1988; R.A. Cooper, pers. comm. 1994). This is an unusually high first appearance of the genus and may lend support to the conclusion of Ripperdan and others (1993) based on carbon isotope data that the lower part of the *Cordylodus lindstromi* Zone may be missing at Dayangcha. In terms of trilobites, *Ig. jilinensis* appears within the *Yosimuraspis* Assemblage Zone of Qian (1986). Specimens of *Leioptegium (Manitouella) floodi*, a cosmopolitan species, first appear about 3 m below the first appearance of *Ig. jilinensis*. It co-occurs with the biostratigraphically useful conodont *Cordylodus lindstromi* s.s. and with the first appearance of *Drepanoistodus expansus* (Chen and Gong, 1986) a characteristic local Chinese taxon. Thus, *Ig. jilinensis* appears slightly later in China than *Ig. fluctivagus* in North America with respect to graptolites, but the base of its range may be truncated.

IAPETOGNATHUS LANDINGI new species

Pl. 15, Figs. 1a–4g; Pl. 16, Figs. 1a–4f;
Pl. 17, Figs. 1a–4e; Pl. 18, Figs. 1a–4e;
Pl. 19, Figs. 1a–4f; Pl. 20, Figs. 1a–4f

v. *Iapetognathus preaengensis* LANDING. SEO and ETHINGTON, 1993, Pl. 1, figs. 6, 7.

Material studied. 55 elements.

Etymology. In honour of Ed Landing, the author of the genus *Iapetognathus*.

Diagnosis. Septimembrate apparatus with a ramiform-ramiform configuration in which element types S (Sc, Sb, Sd), X (Xa, Xb) and P (Pb, Pa) have been identified. All elements ramiform with a large, inwardly directed anterior process supporting up to 10 denticles. Posterior process generally absent or reduced, although denticles present on some elements. Cusp of S elements is large, laterally compressed and erect to posteriorly inclined, with a prominent inner margin costa. P element cusp is prominent, but costae are reduced in prominence. Albid tissue in cusp and denticles; base mostly hyaline. Basal cavity deeply excavated under the cusp of all elements and extends under the processes. All elements with well developed striae on cusp and denticles; striae extend to the basal margin in some elements. Major process (anterior) more blade-like than the bar-like processes of other species of the genus.

Description. Multimembrate apparatus in which seven elements (Sc, Sb, Sd, Xa, Xb, Pb and Pa) are recognized. All elements are ramiform with a long, denticulate anterior process, as well as a short posterior projection or process which may be denticulate. The cusp of the S elements is roughly triangular in cross-section, with keels on the anterior and posterior margins and a large costa on the inner-lateral side. The cusp of the X and P elements is generally laterally compressed.

The S elements all follow a similar morphologic plan with a long anterior process that is deflected slightly inward and supports up to 8 to 10 discrete denticles that may be laterally appressed near the base. The denticles are sub-triangular to sub-round in cross section and bent slightly inward. The outer lateral surface of the denticle is flattened parallel to the face of the process. The cusp is laterally compressed with keeled anterior and posterior margins; it has a carina, best developed in the Sc and Sd elements, on the inner lateral face. In oral view (Pl. 15, fig. 4c; Pl. 16, Fig. 4c; Pl. 17, Fig. 4a), the angle formed between the inner carina and the posterior edge of the cusp is less than that formed with the anterior edge. The tip of the cusp is curved inward over the carina. In cross section, the upper part of the cusp is triangular. On some S elements there is a low rounded carina developed on the lower part of the outer face of the cusp process. The surface of the element is striate, most prominently on the cusp and denticles.

The Sc, Sb and Sd elements are distinguished by the morphology of the posterior to inner lateral part of the element. In the Sc element the inner lateral carina is well developed, sharp edged and simple, and it is a strong feature, projecting inward like a truncated inner lateral process (Pl. 15, Fig. 4c). In the Sb element the carina is present but it is rounded and bent more toward the posterior margin. In oral view (Pl. 16, Fig. 4e) the carina may extend further in a posterior direction than does the keeled posterior edge of the cusp. In the Sd element the carina is sharp and inwardly directed, like the Sc element, but there is a secondary carina that develops on the lower part of the cusp and extends to the basal margin (Pl. 17, Fig. 2a). This secondary carina projects inward and posteriorly, expanding the basal margin in a fashion similar to that observed in the Sb element. Also, in the Sd element the keeled posterior margin of the cusp is sharp and bent slightly outward at the base, like the posterior margin of the Sd element of *Ig. aengensis*.

The X elements have a large blade-like anterior process and a reduced posterior process. The Xa (Pl. 18, Figs. 1a–4e) element has 8 to 10 laterally compressed denticles on the anterior blade that vary from closely appressed to being discrete for much of their height. The cusp is slightly taller than the blade denticles and is asymmetrical with

a rounded rib on the inner side. The cusp, like all elements of the species, bends slightly inward. The posterior process is short and usually supports two denticles that are of variable height. The basal surface is most deeply excavated under the cusp and has a prominent groove extending under the length of the anterior process. The base of the posterior process is shallowly excavated, wider aborally than the anterior groove and extends to the rounded posterior margin.

The Xb element (Pl. 19, Figs. 1a–f) also has a blade-like anterior process that supports at least 5 denticles. The denticles and cusp are laterally compressed and are less prominent than those of the Xa element. The posterior process consists of two denticles in which only the apices are defined. The aboral surface is similar to that of the Xa element except for the posterior margin which is broadly rounded but does not extend as far posteriorly.

The Pb element has a prominent anterior blade with at least 6 closely appressed, laterally flattened denticles. The cusp is slightly larger than the rest of the blade denticles and there may be two denticles posterior to the cusp. The inner margin of the cusp bears a low carina and the first denticle behind the cusp has a carina that is directed inwardly and posteriorly giving the appearance of a bifurcation of the posterior margin (Pl. 19, Fig. 4f).

The Pa elements (Pl. 20, Figs. 1a–4f) have a large laterally compressed cusp with a short anterior process that has two or three denticles. The cusp has a low costa on both inner and outer sides. The outer margin costa is larger and extends to the basal margin forming a slight outward flare, or spur, of the basal margin. The inner basal margin has no comparable flare and the element appears slightly bowed outward. The anterior process denticles are laterally compressed, pointed and discrete. Both cusp and denticles are striate, with striae extending to near the basal margin, especially on the cusp. The base of the element is excavated under both cusp and process.

Remarks. Elements of *Iapetognathus landingi* are morphologically more closely similar to elements of *Ig. aengensis* than to other species of the genus. Both species have elements with large anterior processes. The S elements of both species are especially similar in general shape and the relationship of cusp to the anterior process.

Geographic Distribution. *Iapetognathus landingi* is known from Colorado and Utah, U.S.A.

Stratigraphic Range. This species is known from the *Rossodus Manitouensis* Zone.

IAPETOGNATHUS SPRAKERSI Landing

Pl. 21, Figs. 1a–5e

Iapetognathus sprakersi LANDING, In LANDING, WESTROP and KNOX, 1996, p. 672, figs. 5.1–5.3.

- Cordylodus drucei* MILLER. POHLER and ORCHARD, 1990, p. 16, Pl. 2, figs. 7, 8 only (non fig. 6).
 v. , *Iapetognathus* cf. *I. preaengensis* Landing. TAYLOR, REPETSKI, and ORNDORFF, 1992, p. 412.
 v. *Iapetognathus* n. sp. 2 MILLER and STITT, 1995, p. 108; v. MILLER and TAYLOR, 1995 p. 111.
 v. *Iapetognathus* n. sp. TAYLOR, REPETSKI, and ROEBUCK, 1996, p. 156–157, Fig. 6A.

Material studied. 32 elements.

Diagnosis. Multimembrate apparatus of ramiform elements, in which only the three S type element, Sc, Sb and Sd, are now recognized. All elements with a postero-laterally directed outer lateral process that is short and usually supports one or two long discrete denticles. The cusp and denticles are tall, free-standing and slightly recurved posteriorly. The cusp is ovate in cross section, and strongly laterally compressed to near the base. Lateral process is low and attached only near the base of the cusp. The process denticles are compressed in plane of process. The basal cavity is shallow and broad. The junction of the outer lateral process with the cusp is low, thin and fragile. Albid tissue is confined to cusp and denticles.

Description. Multimembrate apparatus, in which three element types, Sc, Sb and Sd are recognized. The elements have a long posteriorly recurved cusp that is biconvex to ovate in cross section with anterior and posterior keels well developed in the upper part. The anterior keel terminates proximally at the bend point of the cusp, best seen in lateral view, and the lower part of the anterior margin is broadly rounded. The elements have a short outer lateral process that is directed postero-laterally and usually supports no more than one or two long, discrete denticles that are compressed in the plane of the process and posteriorly recurved. The Sc, Sb and Sd elements are differentiated using the presence and extent of a carina on the outer lateral face of the cusp. The Sc element has no carina developed, The Sb element has only a short carina leading from the upper surface of the outer lateral process up the face of the cusp. The Sd element has carina similar to that of the Sb element, but it extends up the lateral face of the cusp to near the tip of the cusp.

In the limited material available for study, no P or X elements have been differentiated. As in other species of the genus, symmetrical (Sa) or makelliform (M) elements are apparently absent.

Remarks. This species was described by Landing in Landing and others (1996) based on an element obtained from the Tribes Hill Formation of upstate New York and several from the Garden City Formation of southern Idaho. On that limited material, Landing did not differentiate more than one element type (Landing and others, 1996,

Figs. 5.1–5.3) but with more than 30 elements available from this study, we are able to differentiate three element types.

Iapetognathus sprakersi is differentiated from other species of the genus by the relatively shallow basal cavity, the strong lateral compression of the cusp and the low and fragile connection of the posteriorly directed outer-lateral process. This process is frequently broken away from the cusp at a point between the cusp and proximal process denticle.

Geographic distribution. *Iapetognathus sprakersi* occurs quite widely, but not in great abundance at any one locality. It has been found chiefly in North America, but it also occurs in Russia and Australia (see Table 4). In North America it is known from platform carbonate strata in the northern and central Appalachian Mountains, the southern midcontinent, and much of the western Cordillera. It also has been found in continental slope to basinal facies in western North America, although it is not known whether these represent indigenous occurrences in these facies or postmortem downslope transport of these elements.

Stratigraphic range. *Iapetognathus sprakersi* has a relatively long stratigraphic range compared with other species of the genus. In the Lawson Cove section of Utah (Fig. 1), it ranges through 31.4 m of strata assigned to the House Limestone. Its lowest occurrence is slightly above the base of the *Cordylodus angulatus* Zone, and its highest occurrence is considerably above the base of the thick *Rossodus manitouensis* Zone. The species occurs in several other sections in Texas, Oklahoma, Utah and Nevada (Table 4) within the same biostratigraphic range.

Genus IAPETONUDUS New Genus

Type species. *Iapetonudus ibexensis* new species.

Derivation of name. *Iapeto-* from *Iapetognathus* and *nudus*, from the Latin for naked; in this case lacking processes and denticulation. Thus a naked *Iapetognathus*.

Diagnosis. Multimembrate coniform apparatus including Sc, Sb, Sd and Pa elements. Elements have a laterally compressed cusp, slightly expanded base, and the upper part of the cusp is posteriorly recurved or bent. The anterior margin is broadly rounded and a keel, present on the upper part of the cusp, terminates abruptly some distance above the base. The surface is smooth. All elements lack clear processes and any sign of denticle development but one or two keels extend from cusp to the aboral margin, marking the line of proto-processes.

Remarks. Elements of *Iapetonudus* are morphologically similar to those of *Iapetognathus fluctivagus*, but lack any indication of denticle development or lateral processes. In the seven elements recovered in this study it is possible to

recognize four element types by comparing them with the morphologically similar, but denticulate, elements of *Iapetognathus fluctivagus*.

IAPETONUDUS IBEXENSIS new species

Pl. 22, Figs. 1a–4g; Pl. 23, Figs. 1a–3g

Material studied. 7 elements (Sc-2, Sb-1, Sd-1, Pa-1, undifferentiated-2).

Etymology. Latin *ibexensis*, from the Ibex area, west-central Utah, where the species was first recognized.

Diagnosis. Same as for the genus.

Description. Multimembrate apparatus in which only four element types (Sc, Sb, Sd and Pa) have thus far been differentiated. All elements have a laterally compressed cusp and one or two proto-processes marked by a keel on the slightly flared base of the element. The surface of the element is smooth, except for the keels. Albid tissue is confined to the cusp.

The S elements are distinguished by a cusp that is laterally compressed and has an outer lateral keel. The Sc element has only a single keel, located on the outer lateral side of the element. The inner lateral margin is rounded toward the base. The keel of the posterior edge of the cusp twists outward and extends as a proto-process to the outer-lateral margin and onto the cusp base. The Sb element is similar to the Sc element but has two proto-process keels. The outer lateral keel is best developed and is seen as a low crest at the basal margin. The inner-lateral keel extends only part-way to the base and is not prominently expressed at the basal margin. The Sd element is also similar but has two prominent keels on the proto-processes that extend nearly to the basal margin.

The Pa element is generally similar to the Sc element, but the plane of compression of the cusp is twisted slightly outward so that the keeled cusp margin points toward the plane of the keeled outer-lateral proto-process. The inner lateral basal margin of the element is broadly rounded.

No Pb or Xa or Xb elements have been recognized for this species. As with *Iapetognathus*, no symmetrical (Sa) or makelliform (M) elements have been found.

Remarks. The gross morphology of each of the elements of *Iapetonudus ibexensis* thus far differentiated is very similar to the comparable element type of found in *Iapetognathus fluctivagus*, except for the lack of a denticulate lateral process. In *Iapetonudus ibexensis* the process is effectively reduced to a keel or carina extending along a slightly elevated ridge, a proto-process, on the side of the base of the cone. In *Iapetognathus fluctivagus* this structure is extended outward from the core of the cone, as a lateral extension or process, and it develops denticulation. The flexure point on the anterior margin of the cusp is

identical in similar elements of the two species. The locations of the keeled proto-processes of *Iapetonudus* are comparable with the locations of the denticulate processes of *Iapetognathus fluctivagus*. Based on the apparent similarity of the apparatuses of *Iapetonudus ibexensis* and *Iapetognathus fluctivagus*, we expect the full apparatus structure of *Iapetonudus ibexensis* to be composed of seven element types.

It is apparent that *Iapetognathus* evolved from *Iapetonudus* with the development of denticulation along the keel of the proto-processes and the outward growth of processes. None of the elements of *Iapetonudus* that we have examined show any sign of incipient denticulation, but we have seen very few specimens. *Iapetonudus* and *Iapetognathus* co-occur in the stratigraphically oldest samples thus far collected from the *Iapetognathus* Zone.

Geographic distribution. *Iapetonudus ibexensis* is known only from the United States. Of seven elements in our collections, five are from the Lawson Cove section, Utah (Table 6, locality 1); one element is from the Lange Ranch Section, Texas and one from the Chandler Creek Section, Oklahoma (see Table 6).

Stratigraphic range. This species occurs only in the lower part of the *Iapetognathus* Zone. In the Lawson Cove section, it is found in three samples from the lower 0.9 m of the *Iapetognathus* Zone; the upper sample is from the bed that yielded a large collection of elements of *Ig. fluctivagus* (sample 438); this bed also yielded the olenid trilobite *Juuyaspis borealis*. In Oklahoma the single element is from the base of the *Iapetognathus* Zone and the element from Texas occurs 0.6 m above the base of the *Iapetognathus* Zone.

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drafted Figure 2. The manuscript was improved through reviews by Scott Ritter (Brigham Young University), Sandy McCracken (Geological Survey of Canada) and an anonymous reviewer.

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PLATE 1

Iapetognathus aengensis (Lindström)
Sc element

Specimens are from a sample of the Ceratopyge Limestone at the Ånga Quarry, Stora Backar, Västergötland, south-central Sweden, collected for topotype material from Bed 5 of Lindström (1955) All figures X60

1. Right element (USNM 498914). 1a. aboral view, 1b. oral view, 1c. oblique inner-lateral view, 1d. oblique posterior-outer lateral view, 1e. outer lateral view, 1f. oblique oral-inner lateral view
2. Right element (USNM 498915). 2a. oblique inner lateral view, 2b. oral view, 2c. posterior-outer lateral view, 2d. outer lateral view
3. Right element (USNM 498916). 3a. outer lateral view, 3b. oral view, 3c. oblique oral-inner lateral view.
4. Left element (USNM 498917). 4a. oral view, 4b. aboral view, 4c. oblique oral-inner lateral view, 4d. outer lateral view, 4e. posterior view, 4f. anterior view, note strong curvature of cusp just above the level of the anterior process
5. Left element (USNM 498918). 5a. oral view, 5b. aboral view, 5c. oblique oral-inner lateral view, 5d. oblique anterior-inner lateral view, 5e. posterior view, 5f. outer lateral view

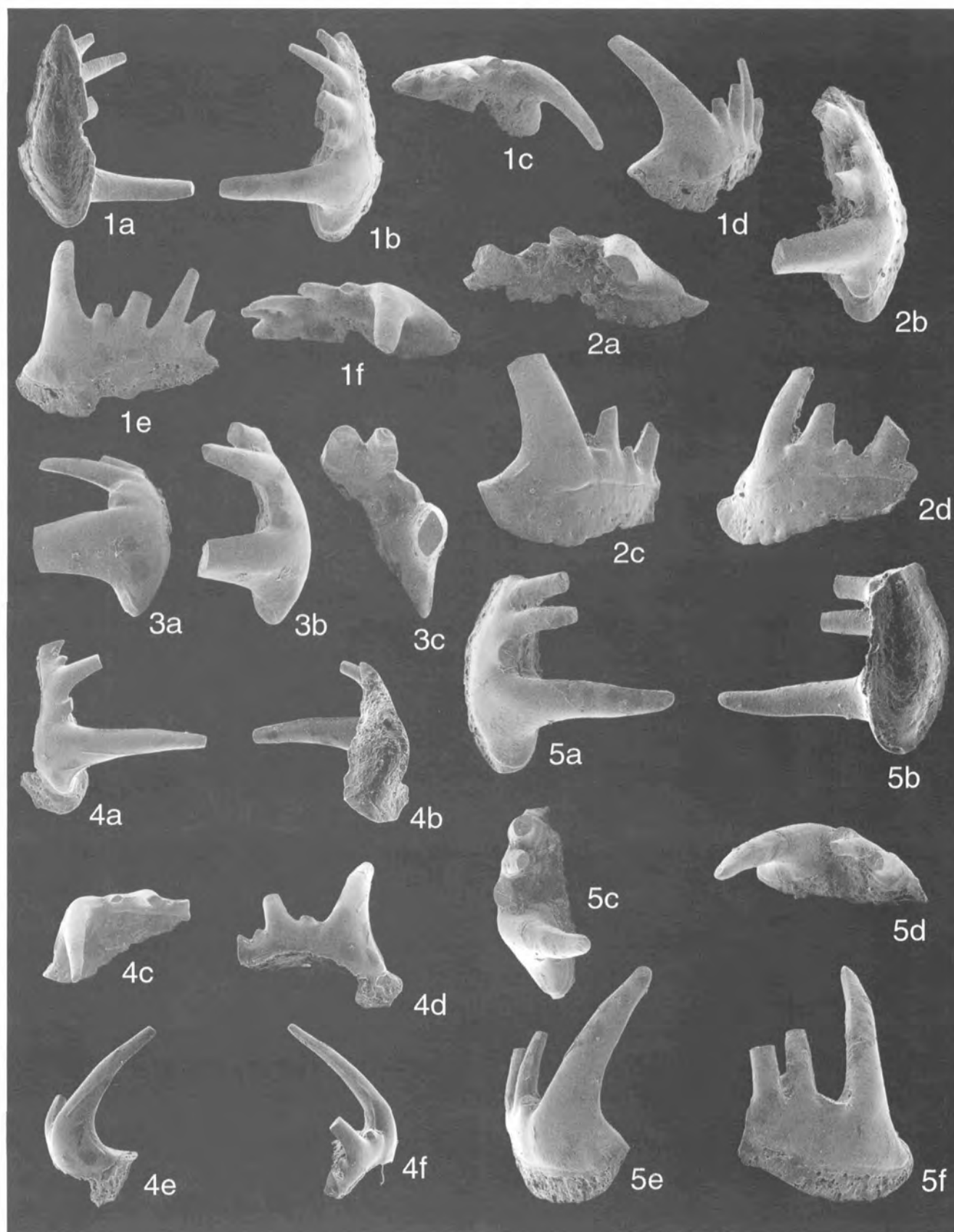


PLATE 2

Iapetognathus aengensis (Lindström)

Sb element

Specimens are from a sample of the Ceratopyge Limestone at the Änga Quarry, Stora Backor, Västergötland, south-central Sweden, collected for topotype material from Bed 5 of Lindström (1955).

1. Right element (USNM 498919), all views X105. 1a. anterior view, 1b. oral view, 1c. posterior view, 1d. oblique outer lateral view.
2. Left element (USNM 498920), all views X110. 2a. oblique oral-inner lateral view, 2b. oral view, 2c. aboral view, 2d. posterior view, 2e. anterior view, 2f. outer lateral view.
3. Left element (USNM 498921), all views X110. 3a. oblique oral-inner lateral view, 3b. oral view, 3c. aboral view, 3d. outer lateral view, 3e. posterior view, 3f. anterior view.
4. Right element (USNM 498922), all views X95. 4a. oblique posterior-inner lateral view, 4b. oblique inner lateral view, 4c. inner lateral view, 4d. aboral view, 4e. oral view, 4f. oblique posterior-outer lateral view, 4g. outer lateral view.

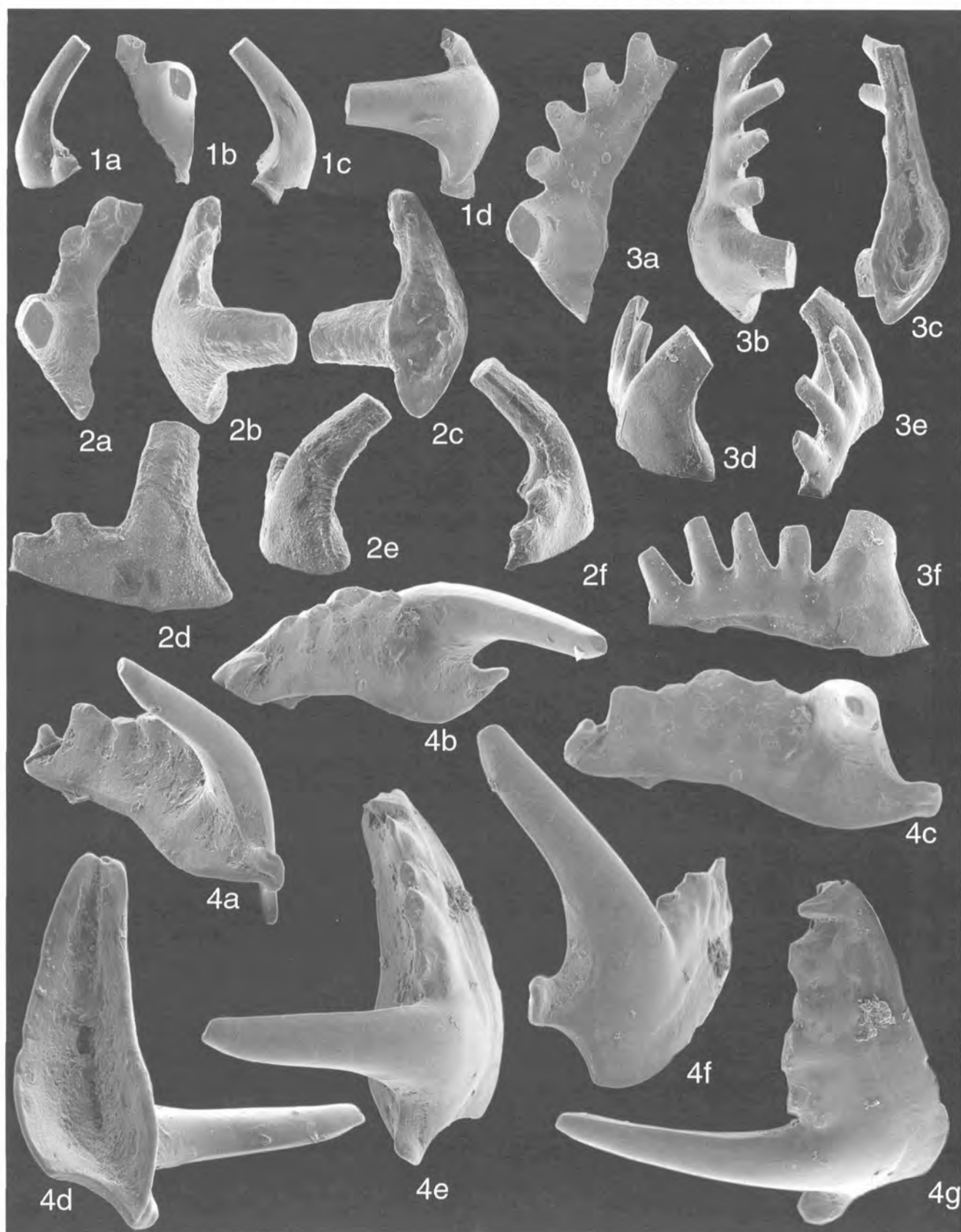


PLATE 3
Iapetognathus aengensis (Lindström)
Sd element

Specimens are from a sample of the Ceratopyge Limestone at the Ånga Quarry, Stora Backor, Västergötland, south-central Sweden, collected for topotype from Bed 5 of Lindström (1955).

1. Left element (USNM 498923), all views X70. 1a. outer lateral view, 1b. oral view, 1c. aboral view, 1d. oblique oral-inner lateral view, 1e. outer lateral view, 1f. oblique anterior-inner lateral view.
2. Left element (USNM 498924), all views X70. 2a. oral view, 2b. aboral view, 2c. oblique inner lateral view, 2d. anterior view.
3. Right element (USNM 498925), all views X60. 3a. oral view, 3b. aboral view, 3c. inner lateral view, 3d. outer lateral view, 3e. posterior view.
4. Left element (USNM 498926), all views X90. 4a. oral view, 4b. oblique inner lateral view, 4c. aboral view, 4d. posterior view, 4e. anterior view.

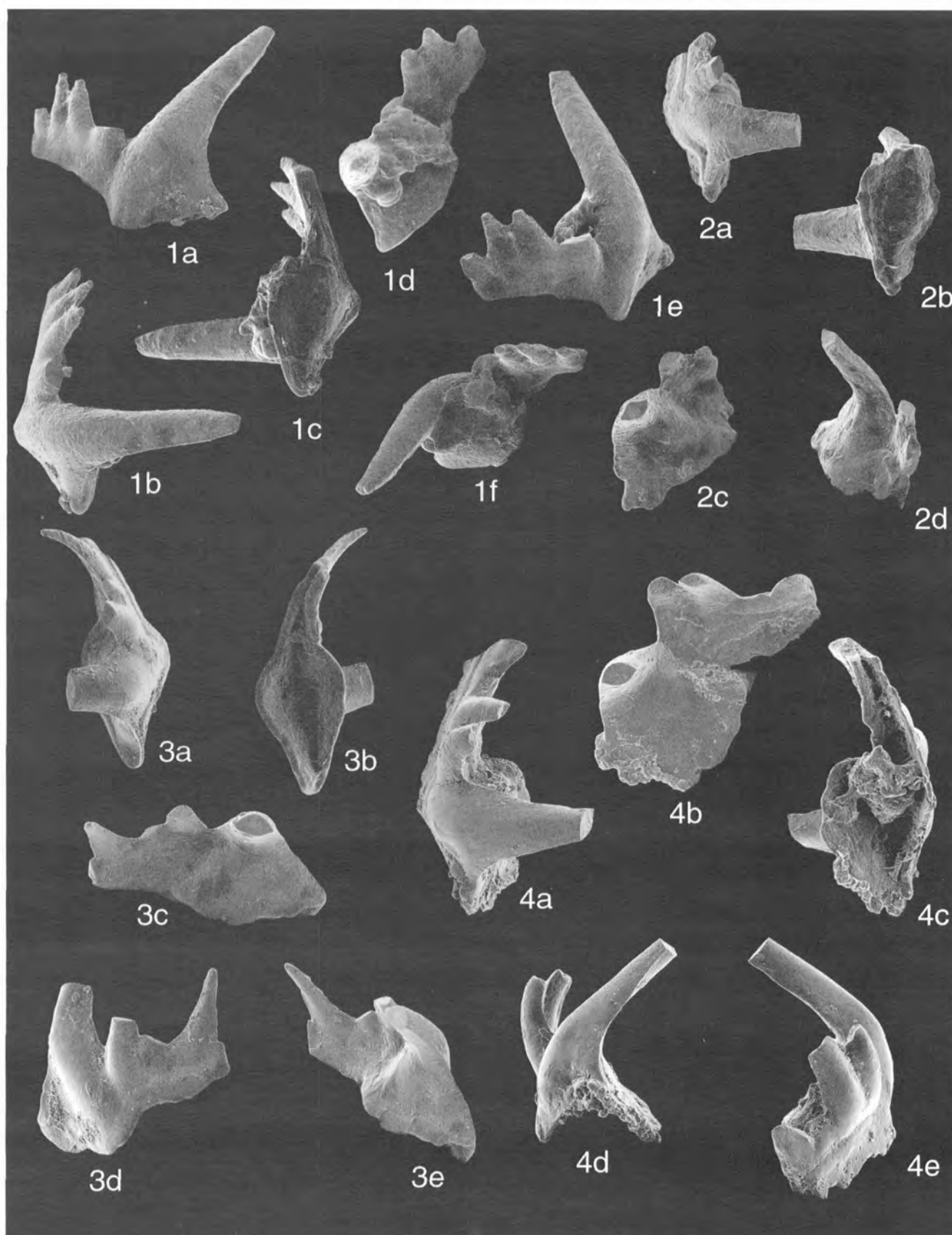


PLATE 4

Iapetognathus aengensis (Lindström)
X and Pb elements

Specimens are from a sample of the Ceratopyge Limestone at the Änga Quarry, Stora Backor, Västergötland, south-central Sweden, collected for topotype material from Bed 5 of Lindström (1955)

1. Right X element (USNM 498927), all views X105. 1a. oral-outer lateral view, 1b. inner lateral view, 1c. aboral view, 1d. posterior view, 1e. oblique posterior-view, 1f. oral view.
2. Left Pb element (USNM 498928), all views X90. 2a. oral view, 2b. aboral view, 2c. inner lateral view, 1d. outer lateral view, 2e. anterior view, 2f. posterior view.
3. Left Pb element (USNM 498929), all views X110. 3a. oral view, 3b. aboral view, 3c. inner lateral view, 3d. outer lateral view, 3e. posterior view, 3f. anterior view.

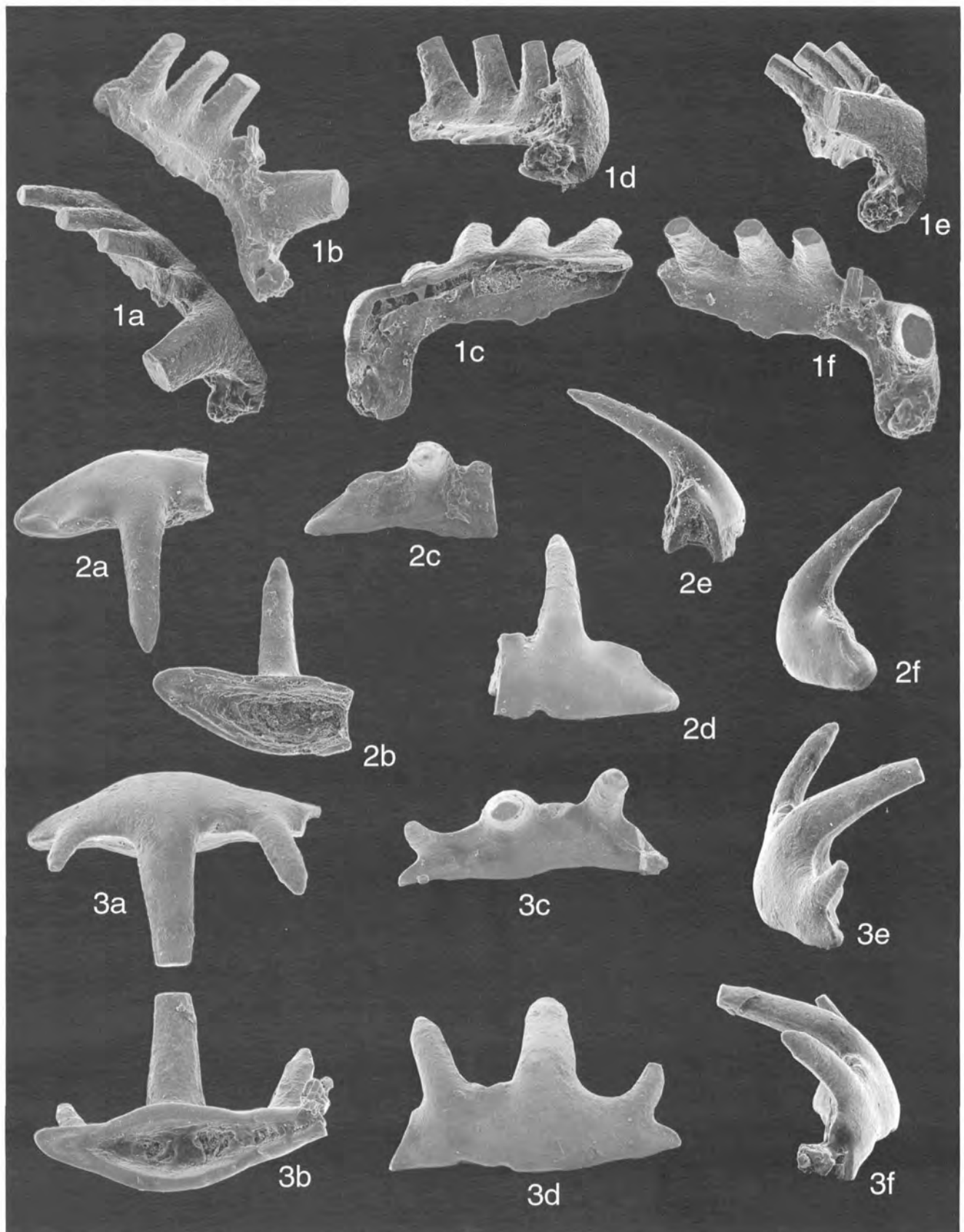


PLATE 5

Iapetognathus aengensis (Lindström)

Pb and Pa elements

Specimens are from a sample of the Ceratopyge Limestone at the Ånga Quarry, Stora Backor, Västergötland, south-central Sweden, collected for topotype material from Bed 5 of Lindström (1955). All figures X120.

1. Left Pb element (USNM 498930). 1a. outer lateral view, 1b. oblique oral-outer lateral view, 1c. oral view, 1d. aboral view, 1e. posterior view, 1f. anterior view.

2. Left Pa element (USNM 498931). 2a. outer lateral view, 2b. oral view, 2c. oblique oral-inner lateral view, 2d. aboral view, 2e. posterior view, 2f. anterior view.

3. Left Pa element (USNM 498932). 3a. oblique oral-outer lateral view, 3b. oral view, 3c. oblique oral-inner lateral view, 3d. aboral view, 3e. anterior view, 3f. posterior view.

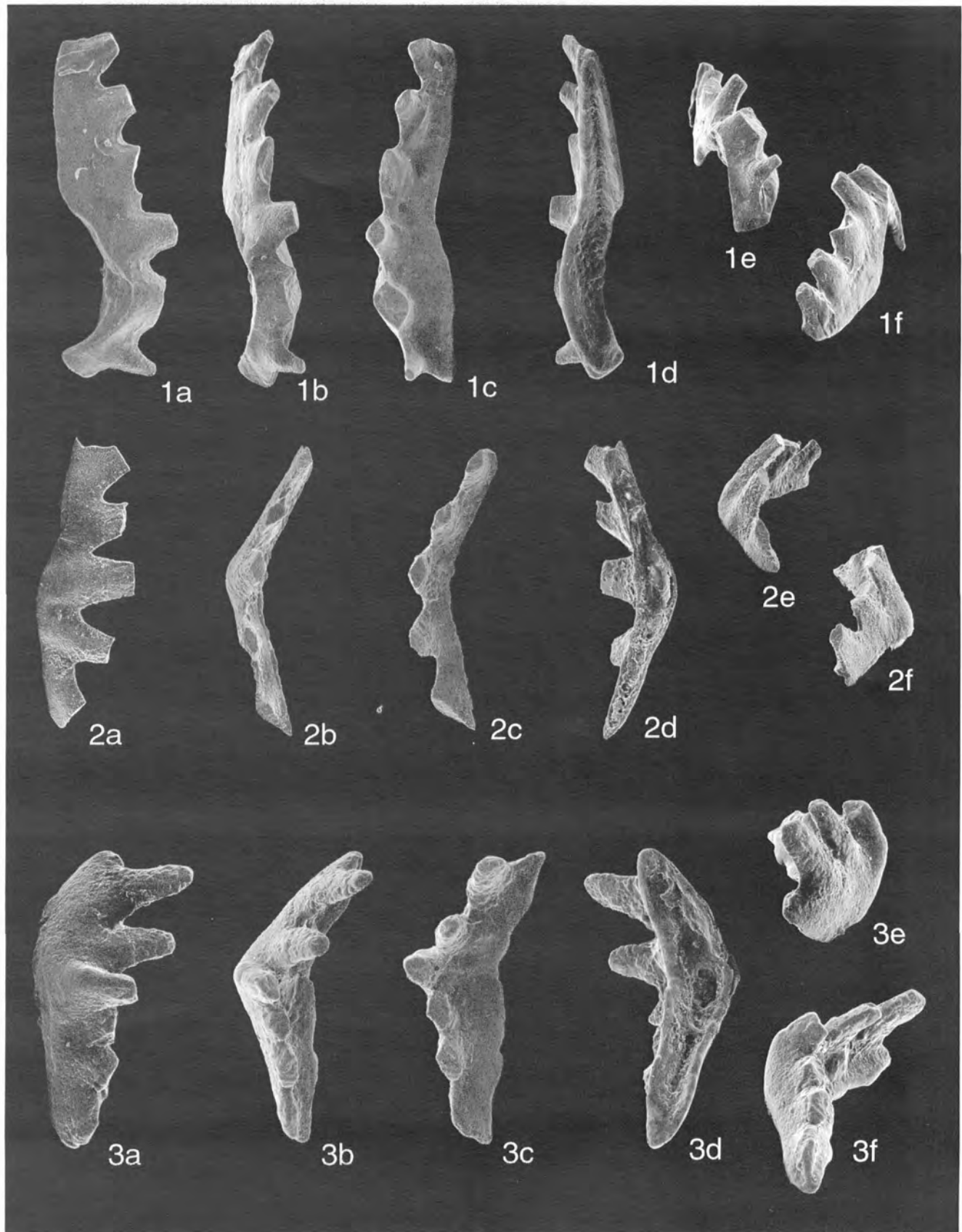


PLATE 6
Iapetognathus fluctivagus new species
Sc element

Specimens are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A.

1. Left element (USNM 498933), all views X185. 1a. oral view, 1b. aboral view, 1c. anterior view, 1d. inner lateral view, 1e.. outer lateral view, 1f. oblique outer lateral view, 1g. posterior view
2. Left element (USNM 498934), all views X165. 2a. oral view, 2b. posterior view, 2c. anterior view, 2d. oblique postero-basal view, 2e. inner lateral view
3. Left element (USNM 498935), all views X175. 3a. oral view, 3b. posterior view, 3c. anterior view, 3d. oblique postero-basal view, 3e. inner lateral view.
4. Right element (USNM 498936), all views X140. 4a. anterior view, 4b. oral view, 4c. inner lateral view, 4d. posterior view, 4e. basal view.
5. Right element (USNM 498937), all views X140. 5a. oral view, 5b. anterior view, 5c. inner lateral view, 5d. oblique postero-basal view.

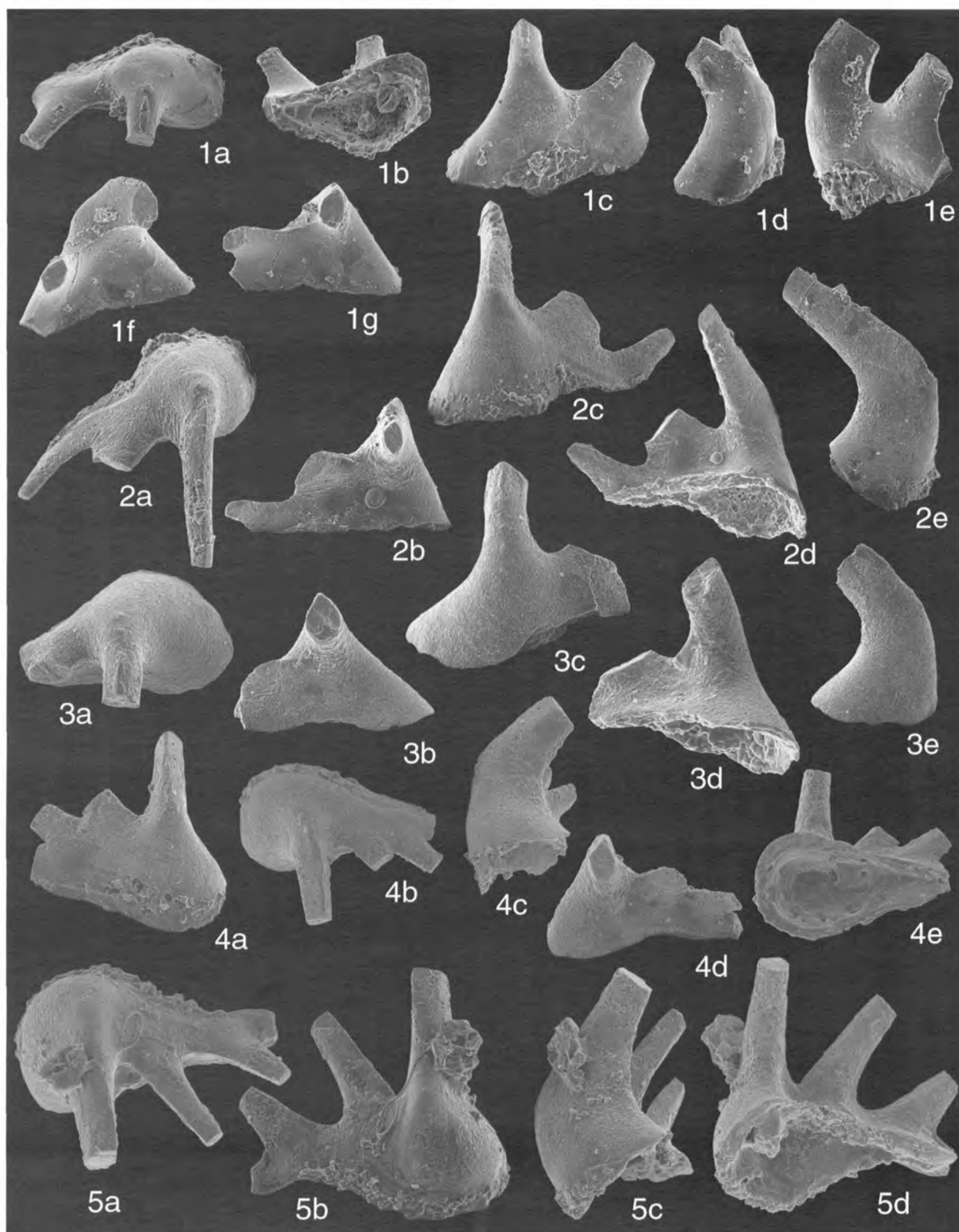


PLATE 7

Iapetognathus fluctivagus new species
Sb element

Specimens are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A.

1. Left element (USNM 498938), all views X125, except as noted. 1a. anterior view, 1b. posterior view, 1c. oblique posterior-oral view, 1d. oral view, 1e.. enlargement (X500) of anterior of cusp (Fig. 1a) showing base of keel and low node.
2. Left element (USNM 498939), all views X110, except as noted. 2a. anterior view, 2b. posterior view, 2c. oblique posterior-oral view, 2d. enlargement (X550) of anterior of cusp (Fig. 2a) showing base of keel and node, 2e. enlargement (X365) of inner lateral view (Fig. 2f), 2f. inner lateral view, 2g. oral view.
3. Right element (USNM 498940), all views X155. 3a. oral view of element with regeneration of broken cusp tip, 3b. posterior view, 3c. oblique postero-basal view.
4. Right element (USNM 498941), all views X115, except as noted. 4a. oral view, 4b. posterior view, 4c. inner lateral view, 4d. outer lateral view, 4e. basal view, 4f. anterior view, 4g. enlargement (X480) of inner lateral view showing base of cusp keel and multiple small nodes on low mound.

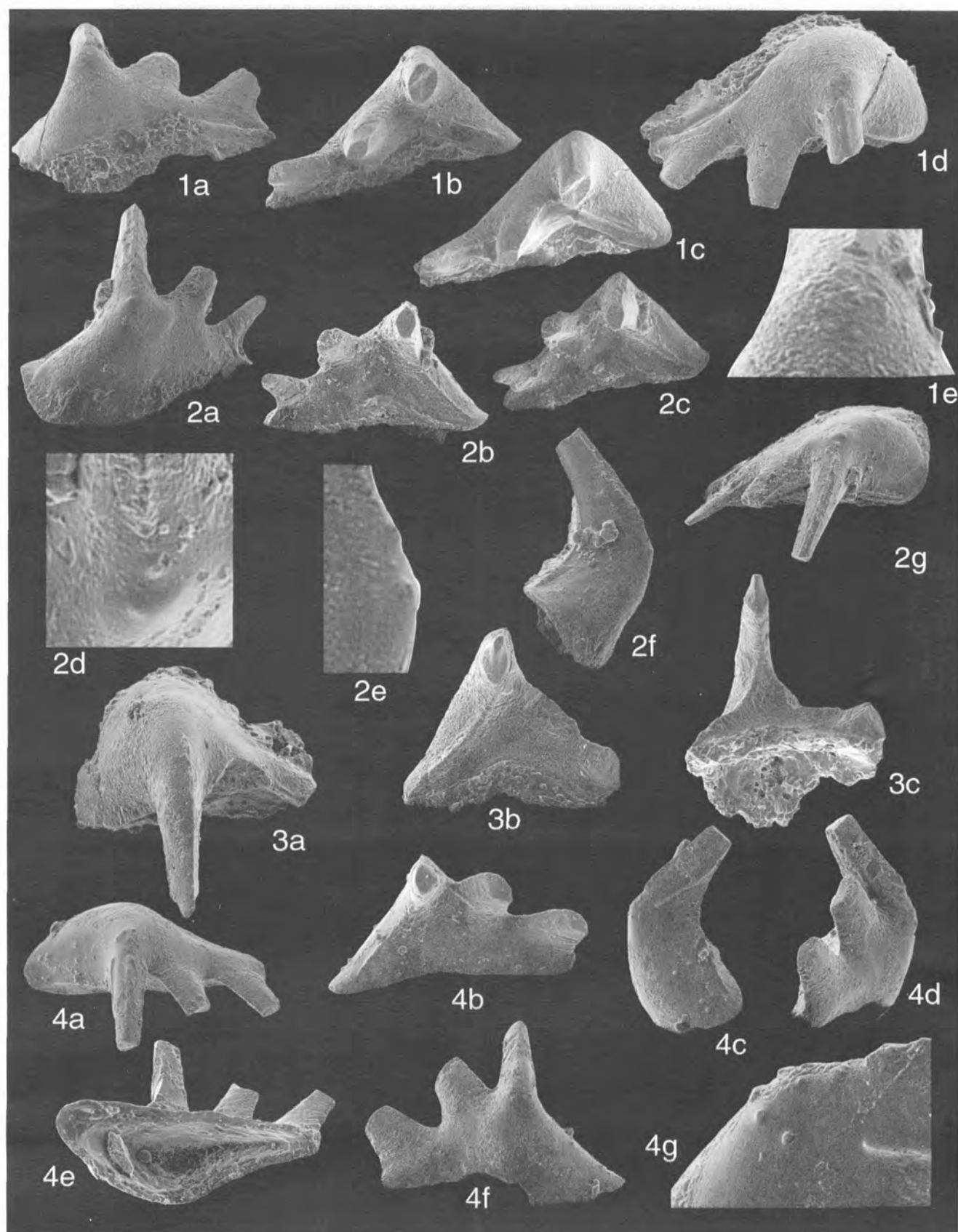


PLATE 8

Iapetognathus fluctivagus new species
Sd element

Specimens are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A.

1. Left Sd element (USNM 498942), all views X140, except as noted. 1a. oral view, 1b. inner lateral view, 1c. anterior view, 1d. outer lateral view, 1d. posterior view, 1e. oblique posterior-oral view, 1f. enlargement (X1260) showing node on anterior margin below the carina.

2. Right Sd element (USNM 498943), all views X180, except as noted. 2a. oral view, 2b. outer lateral view, 2c. inner lateral view, 2d. posterior view, 2e. anterior view, 2f. enlargement (X800) of 2e showing node and base of carina, 2g. enlargement (X800) showing node in profile from the inner lateral view (2c).

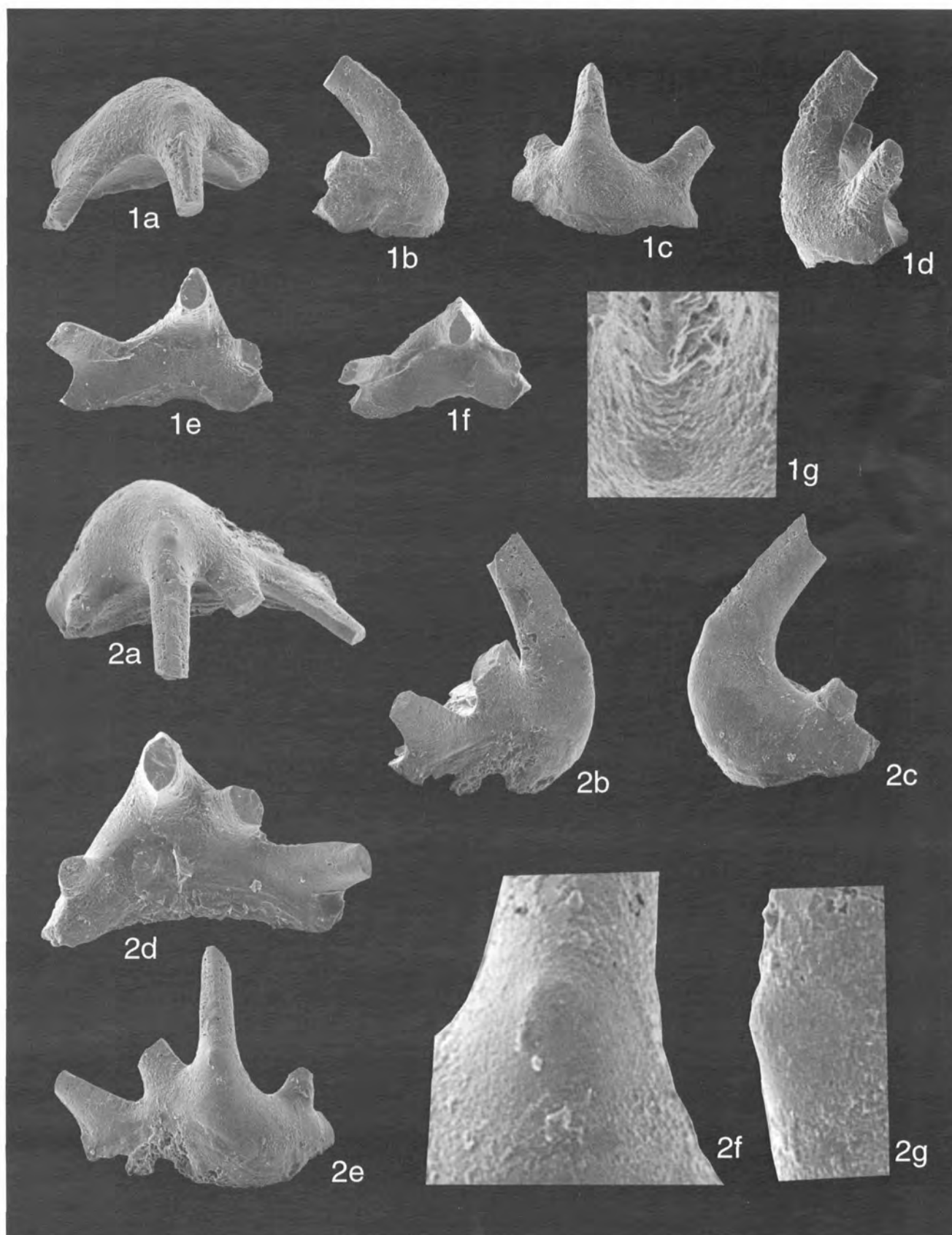


PLATE 9

Iapetognathus fluctivagus new species
Xa and Xb elements

Specimens illustrated in figures 1–5, 7 are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A. Specimen illustrated in figures 6 is from the 435 foot level of the same section.

1. Right Xa element (USNM 498944), all views X160. 1a. anterior view, 1b. oral view, 1c. oblique oral-posterior view, 1d. posterior view, 1e. inner lateral view.
2. Right Xa element (USNM 498945), all views X160. 2a. anterior view, 2b. oral view, 2c. aboral view, 2d. oblique outer lateral-oral view, 2e. oblique oral view, 2f. outer lateral view.
3. Left Xb element (USNM 498946), all views X150. 3a. inner lateral view, 3b. anterior view, 3c. oral view, 3d. oblique oral-posterior view.
4. Right Xb element (USNM 498947), all views X150. 4a. anterior view, 4b. oral view, 4c. oblique oral-posterior view.
5. Left Xb element (USNM 498948), all views X150. 5a. oblique oral-inner lateral view, 5b. oblique oral-posterior view.
6. Right Xb element (USNM 498949), all views X140. 6a. oblique oral-posterior view 6b. oral view.
7. Right Xb element (USNM 498950), all views X150. 7a. oral view, 7b. inner lateral view, 7c. anterior view, 7d. aboral view, 7e. oblique oral-inner lateral view, 7f. oblique inner lateral view.

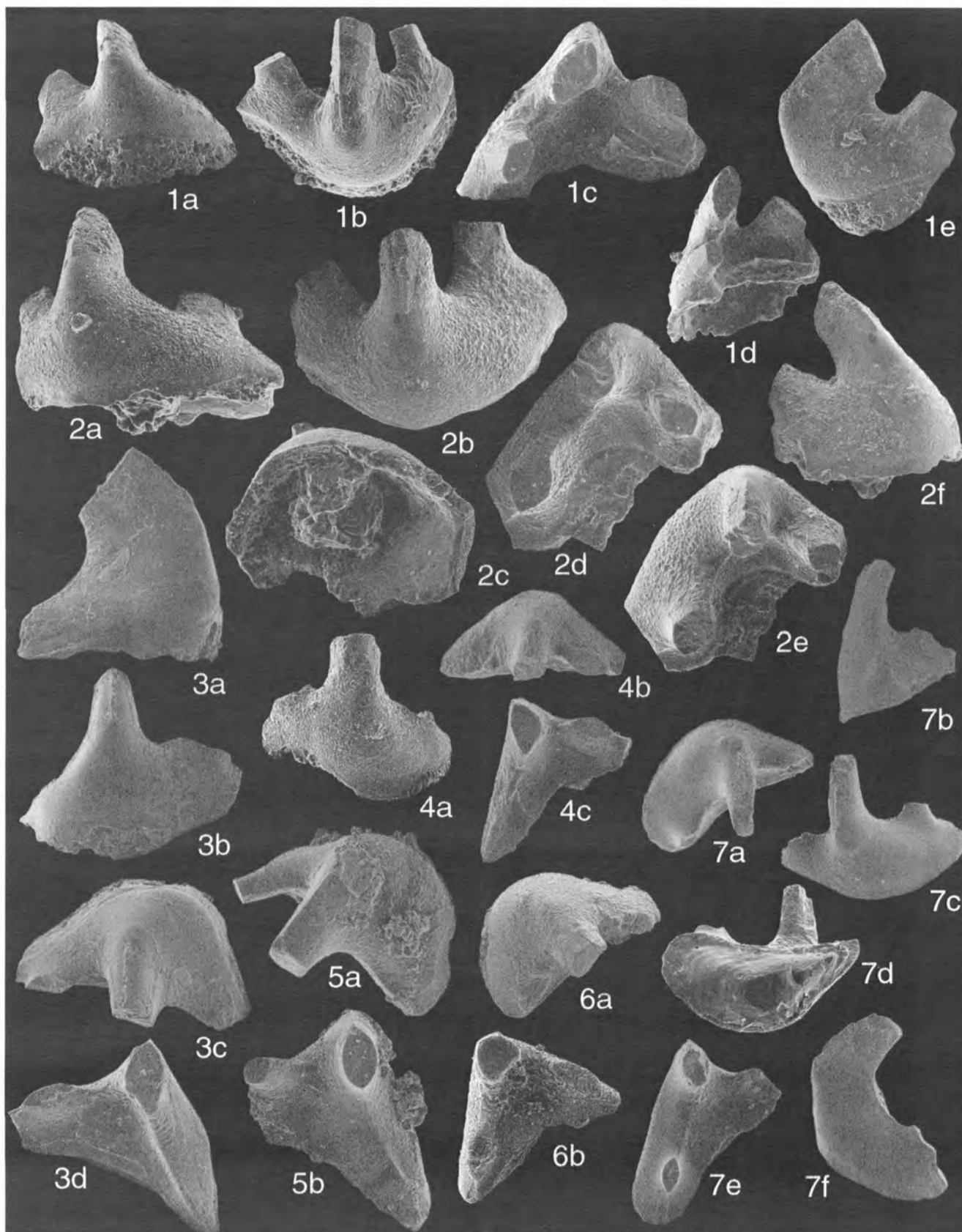


PLATE 10

Iapetognathus fluctivagus new species

Pb element

Specimens are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A. Note that the long axis of the laterally compressed cusp is not twisted, but remains parallel to the inner lateral margin.

1. Left element (USNM 498951), all views X140. 1a. posterior view, 1b. oral view, 1c. inner lateral view, 1d. outer lateral view, 1e. oblique posterior view, 1f. anterior view, 1g. aboral view.
2. Left element (USNM 498952), all views X140. 2a. posterior view, 2b. oral view, 2c. outer lateral view.
3. Left element (USNM 498953), all views X135. 3a. oral view, 3b. posterior view, 3c. anterior view.
4. Right element (USNM 498954), all views X180. 4a. posterior view, 4b. oral view.
5. Right element (USNM 498955), all views X160. 5a. posterior view, 5b. oblique oral-posterior view, 5c. aboral view, 5d. outer lateral view, 5e. inner lateral view, 5f. oblique posterior-oral view, 5g. oral view, 5h. anterior view.
6. Right element (USNM 498956), all views X160, except as noted. 6a. posterior view, 6b. oral view, 6c. anterior view, 6d. aboral view, 6e. outer lateral view, 6f. inner lateral view, 6g. enlargement (X700) of 6c showing base of the crown and the upper part of the attachment cone with its punctate outer surface.

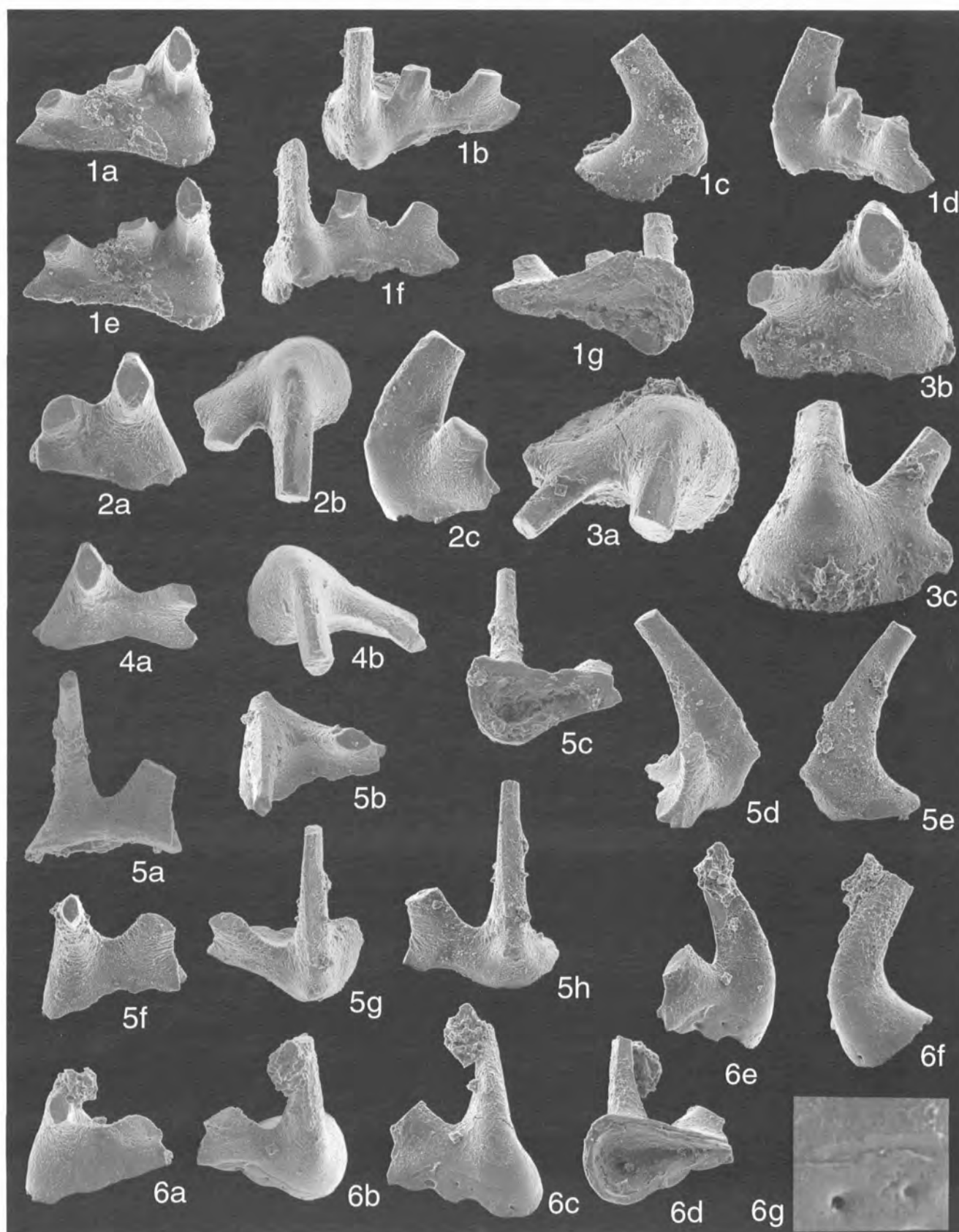


PLATE 11
Iapetognathus fluctivagus new species
Pa element

Specimens are from the 438 foot level of the section described by Miller (1995) at Lawson Cove in the Ibex area, Utah, U.S.A. Note that the long axis of the laterally compressed cusp is twisted outward.

1. Left element (USNM 498957), all views X165. 1a. oral view, 1b. oblique oral-posterior view, 1c. anterior view, 1d. inner lateral view.
2. Left element (USNM 498958), all views X155. 2a. oral view, 2b. posterior view, 2c. oblique posterior-oral view, 2d. outer lateral view, 2e. anterior view, 2f. aboral view, 2g. inner lateral view.
3. Left element (USNM 498959), all views X160. 3a. posterior view, 3b. oral view, 3c. anterior view.
4. Right element (USNM 498960), all views X150. 4a. anterior view, 4b. oral view, 4c. oblique oral-posterior view.
5. Right element (USNM 498961), all views X165. 5a. anterior view, 5b. aboral view, 5c. oral view, 5d. posterior view.
6. Right element (USNM 498962) with well developed attachment cone; all views X160, except as noted. 6a. anterior view, 6b. oral view, 6c. enlargement (X380) of Fig. 6e showing the lower part of the crown, a short band of smooth tissue at the very base of the crown and the overgrowth covered attachment cone, 6d. inner lateral view, 6e. outer lateral view, 6f. posterior view, 6g. oblique posterior-oral view, 6h. aboral view.

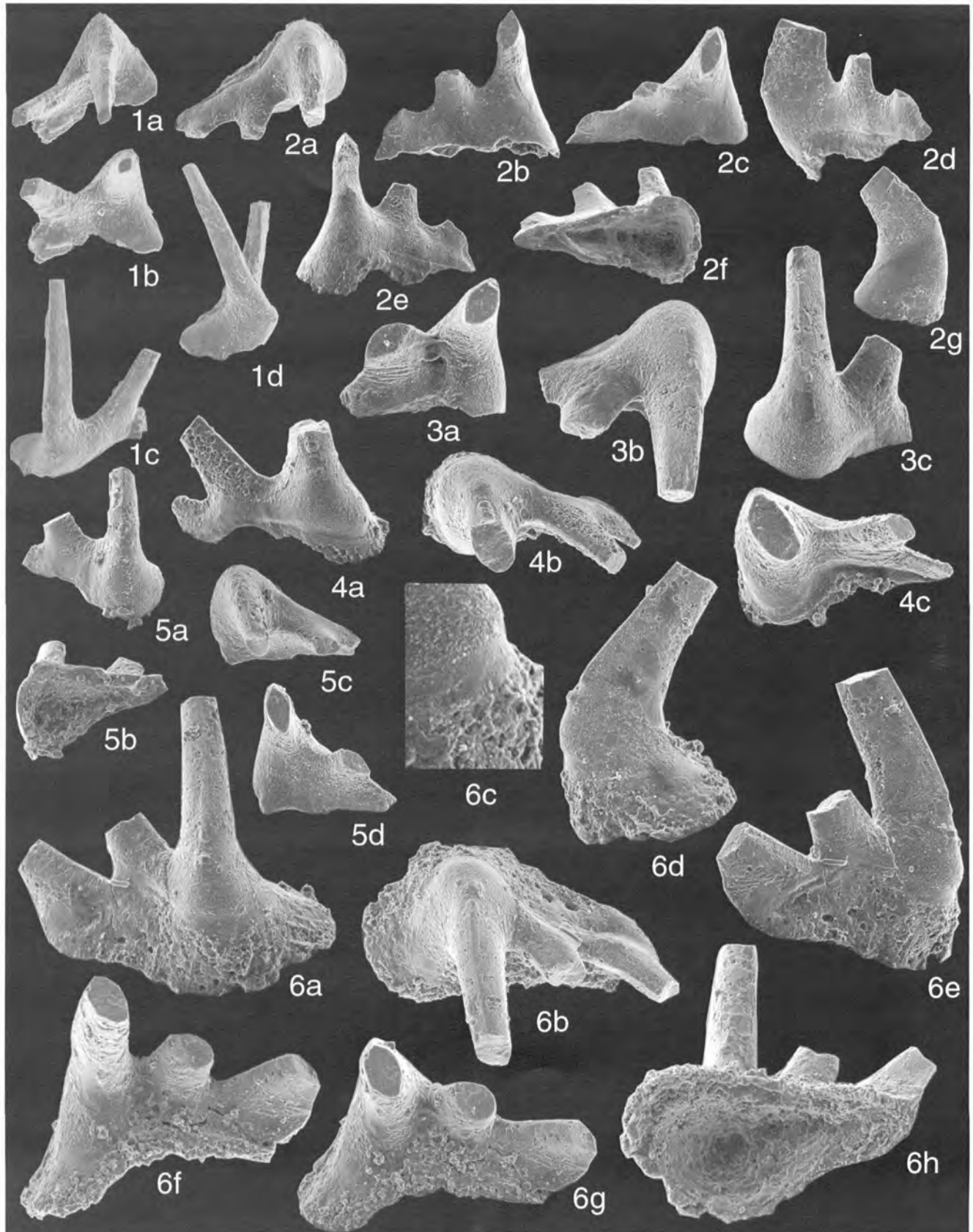


PLATE 12

Iapetognathus jilinensis new species
Sc element

Specimens are from the Xiaoyangqiao Section, Dayangcha, Jilin Province, China. Those illustrated in figures 1 and 4 are from HDA 14-3 and those illustrated in figures 2 and 3 are from HDA 14-2 (Chen and Gong, 1986, Table 17, Nowlan and Nicoll, 1995, Figure 2). Note the well developed attachment cone preserved on all four elements, but especially Fig. 3g.

1. Right element (USNM 498963), all views X90. 1a. oral view, 1b. aboral view, 1c. outer lateral view, 1d. inner lateral view, 1e. anterior view, 1f. posterior view.

2. Right element (USNM 498964), all views X90. 2a. oblique oral-posterior view, 2b. oral view, 2c. outer lateral view, 2d. oblique oral-anterior view, note abrupt truncation of the anterior carina at the base of the cusp, 2e. anterior view, 2f. inner lateral view.

3. Left element (USNM 498965), all views X105. 3a. oral view, 3b. oblique oral-posterior view showing cusp cross-section, 3c. posterior view, 3d. aboral view, 3e. inner lateral view, 3f. outer lateral view, 3g. anterior view.

4. Left element (USNM 498966), all views X100. 4a. inner lateral view, 4b. anterior view, 4c. oblique oral-anterior view, 4d. inner lateral view, 4e. oblique oral-posterior view, 4f. aboral view.

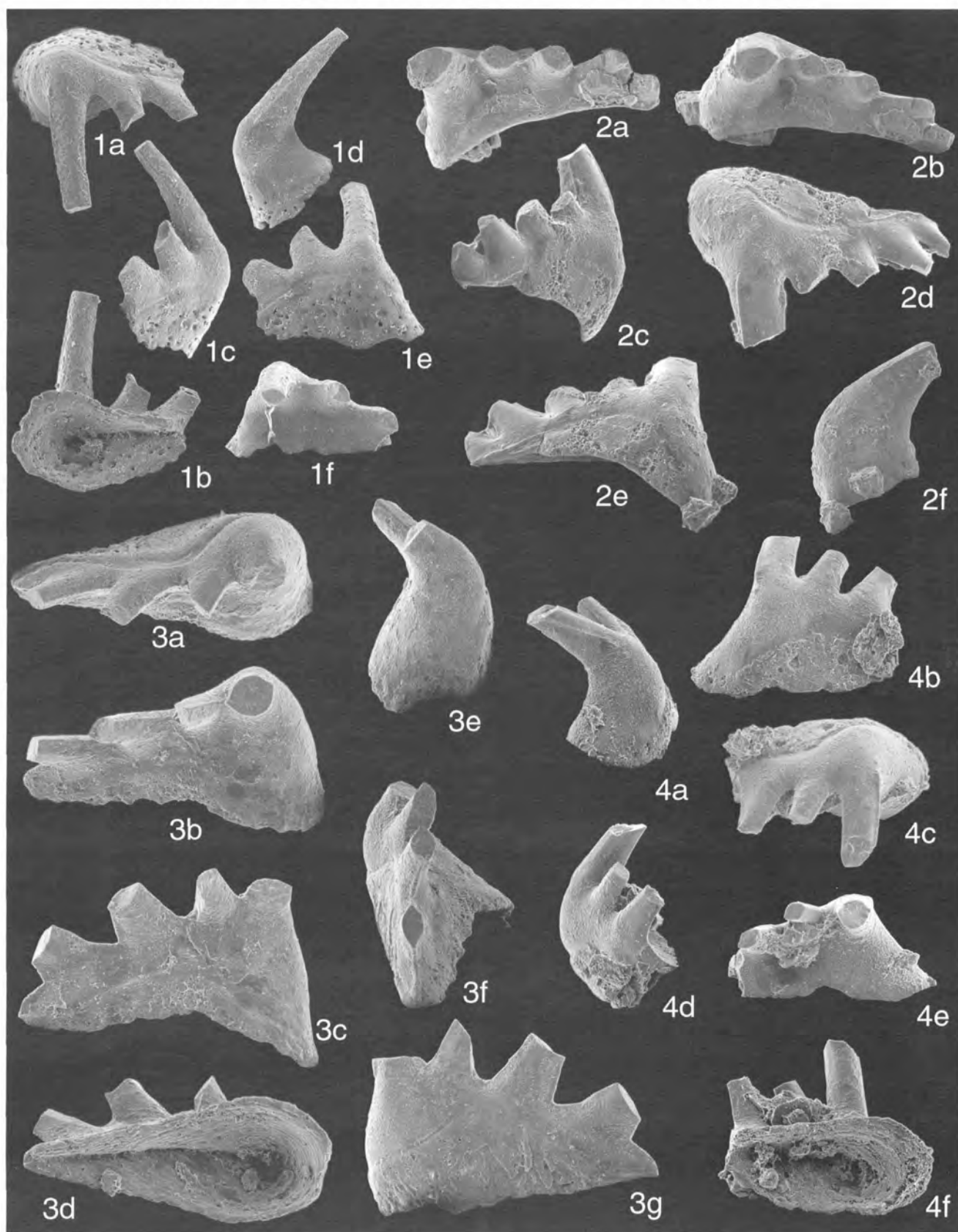


PLATE 13

Iapetognathus jilinensis new species
Sb, Sd and Xa elements

Specimens are from the Xiaoyangqiao Section, Dayangcha, Jilin Province, China. The specimen illustrated in figure 1 is from HDA 14-2 (Chen and Gong, 1986, Table 17; Nowlan and Nicoll, 1995, Figure 2); the specimen illustrated in figure 2 is from a sample taken at 21.62–22.0 m above base of section (Nowlan and Nicoll, 1995), and the specimen illustrated in figure 3 is from a sample taken at 22.0–22.3 m above base of section (Nowlan and Nicoll, 1995, Figure 2).

1. Right Sb element (USNM 498967), all views X60. Note the presence of three carina on the cusp. 1a. oral view, 1b. oblique oral-posterior view, 1c. posterior view, 1d. inner lateral view, 1e. outer lateral view, 1f. aboral view, 1g. oblique posterior view showing carina, 1h. anterior view.

2. Left Sd element (USNM 498968), all views X95. 2a. oral view. 2b. oblique oral-posterior view.

3. Left Xa element (USNM 498969), all views X95. 3a. inner lateral view, 3b. posterior view, 3c. oblique oral-posterior view, 3d. anterior view, 3e. aboral view, 3f. oral view.

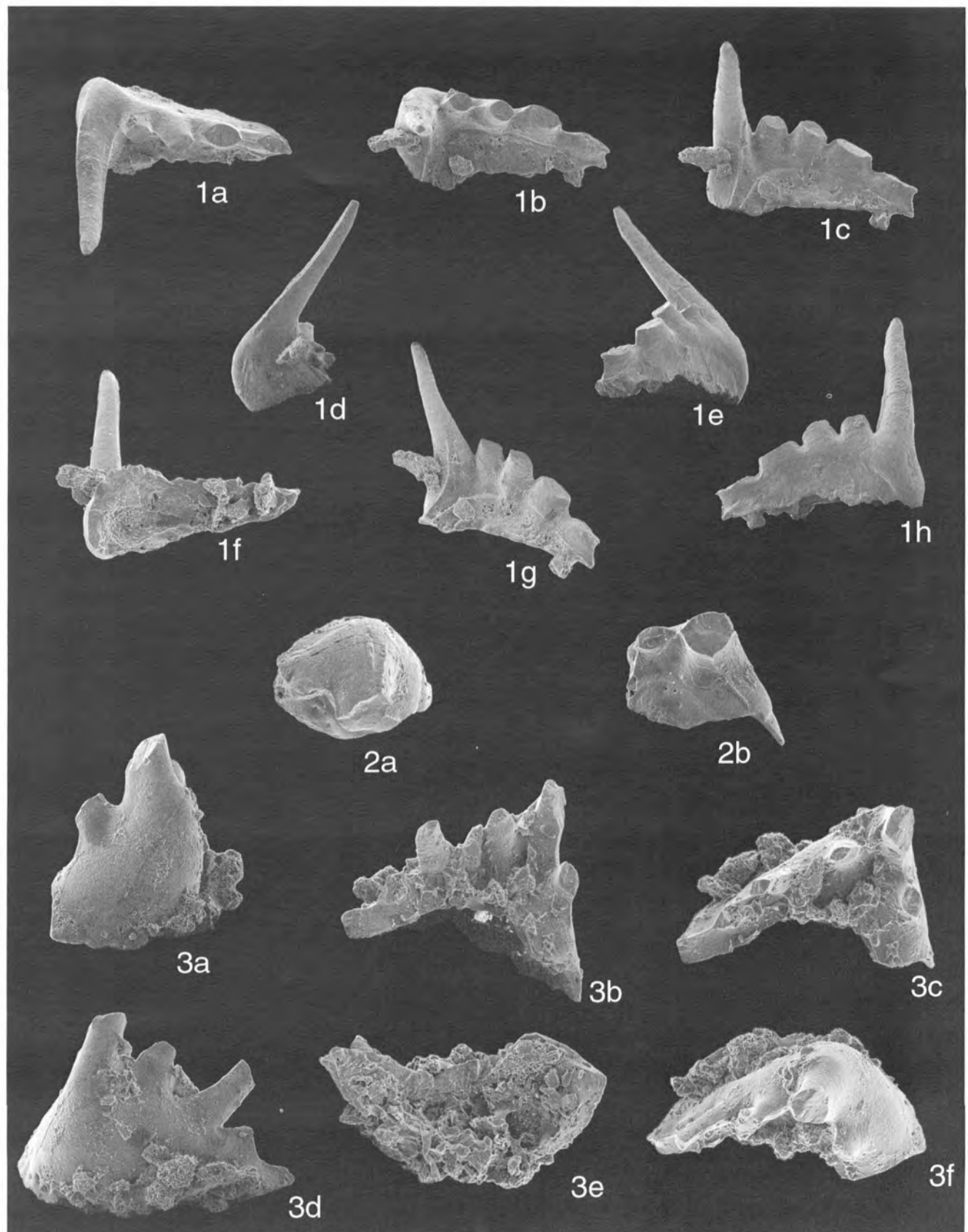


PLATE 14

Iapetognathus jilinensis new species
Pb and Pa elements

Specimens are from the Xiaoyangqiao Section, Dayangcha, Jilin Province, China. The specimens illustrated in figures 1 and 4 are from a sample taken at 21.62–22.0 m above base of section (Nowlan and Nicoll, 1995); the specimen illustrated in figure 2 is from HDA 14-2 (Chen and Gong, 1986, Table 17; Nowlan and Nicoll, 1995, Figure 2) and the specimen illustrated in figure 3 is from a sample taken at 22.0–22.3 m above base of section (Nowlan and Nicoll, 1995, Figure 2).

1. Left Pb element (USNM 498970), all views X150. 1a. oblique oral-posterior view showing cusp cross-section, 1b. oral view.
2. Left Pb element (USNM 498971), all views X160, except as noted. 2a. inner lateral view, 2b. outer lateral view, 2c. oblique oral-posterior view showing cusp cross-section, 2d. oral view, 2e. aboral view, 2f. anterior view, 2g. posterior view, 2h. enlargement (X375) of inner surface of the attachment cone showing the punctate character of the surface.
3. Left Pa element (USNM 498972), all views X155. Oral view showing twisted axis of the cusp, 3b. anterior view, 3c. inner lateral view, 3d. outer lateral view, 3e. posterior view.
4. Right Pa element (USNM 498973), all views X160. 4a. oblique oral-posterior view showing twisted axis of the cusp cross-section, 4b. oral view.

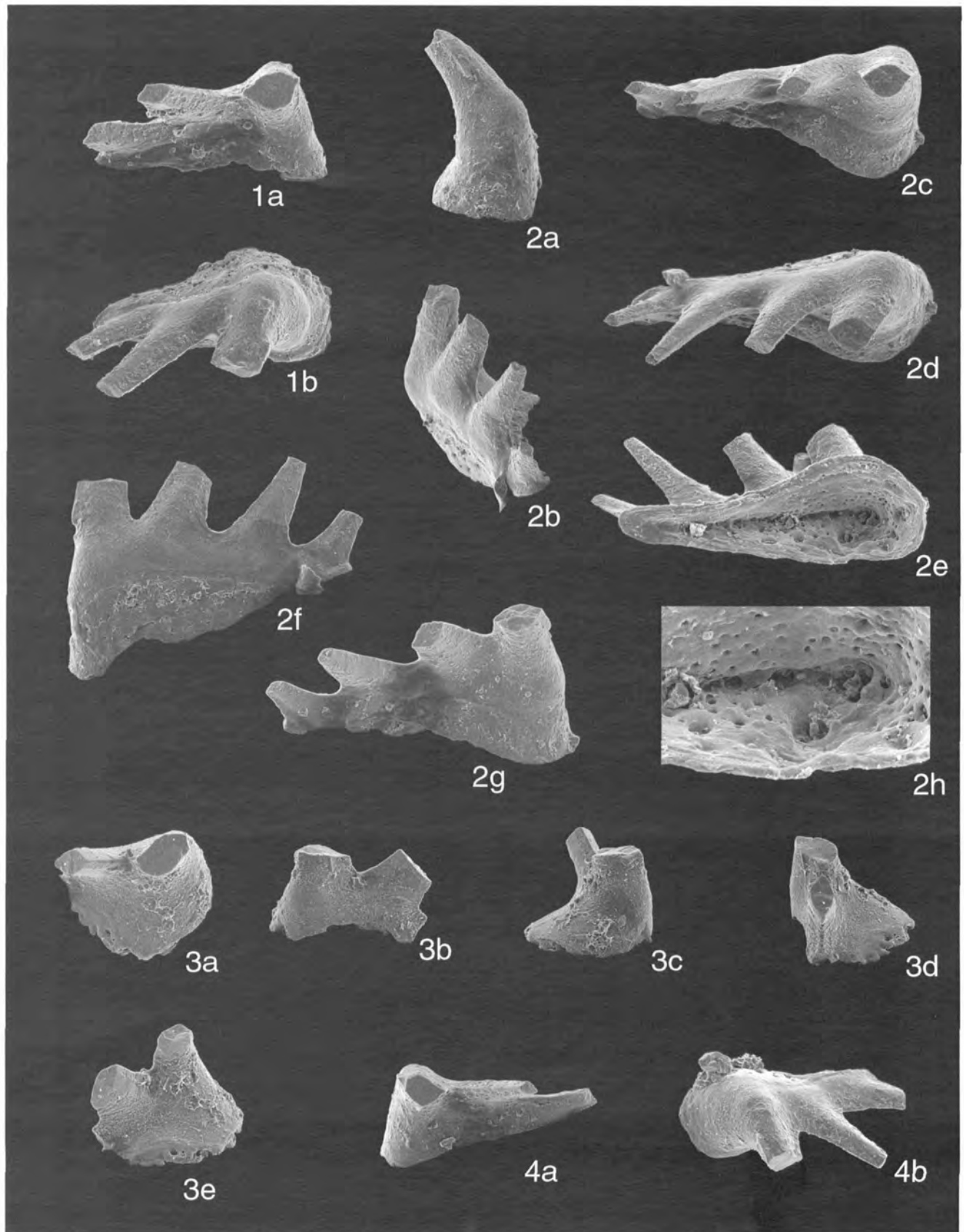


PLATE 15

Iapetognathus landingi new species
Sc element

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959; Seo and Ethington, 1993).

1. Left element (USNM 498974), all views X190. 1a. inner lateral view, 1b. aboral view, 1c. oral view, 1d. outer lateral view, 1e. posterior view, 1f. anterior view

2. Left element (USNM 498975), all views X180. 2a. outer lateral view, 2b. inner lateral view, 2c. oral view, 2d. aboral view.

3. Right element (USNM 498976), all views X220. 3a. oblique oral-inner lateral view, 3b. oral view, 3c. outer lateral view, 3d. inner lateral view, 3e. aboral view, 3f. posterior view, 3g. anterior view.

4. Right element (USNM 498977), all views X190. 4a. oral view, 4b. aboral view, 4c. oblique oral-inner lateral view, 4d. posterior view, 4e. anterior view, 4f. outer lateral view, 4g. inner lateral view.

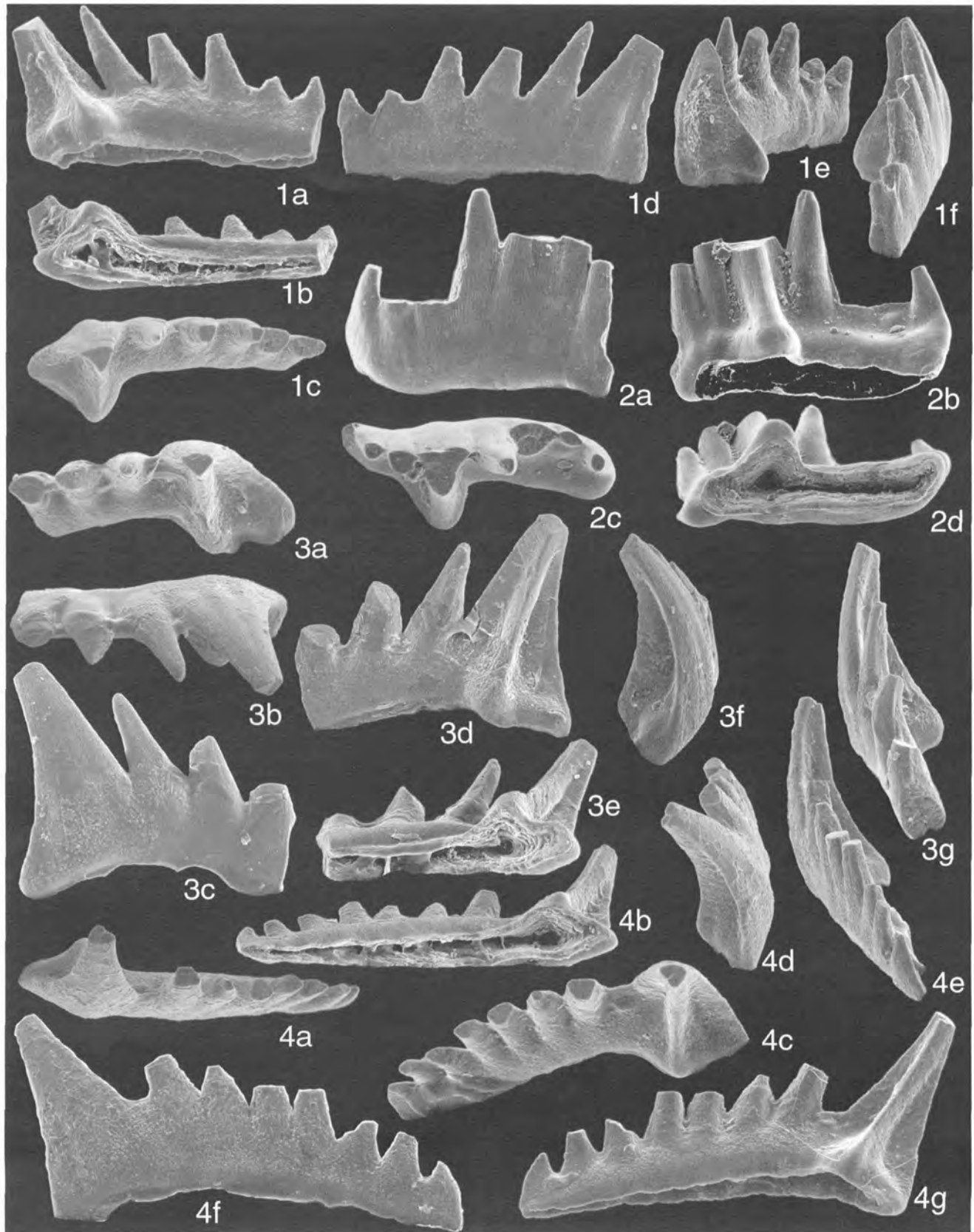


PLATE 16

Iapetognathus landingi new species
Sb element

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959; Seo and Ethington, 1993).

1. Left element (USNM 498978), all views X180. 1a. inner lateral view, 1b. oral view, 1c. aboral view, 1d. outer lateral view.

2. Left element (USNM 498979), all views X180, except as noted. 2a. inner lateral view, 2b. outer lateral view, 2c. aboral view, 2d. oral view, 2e. posterior view, 2f. enlargement (X420) of inner lateral view showing striae pattern of later healing growth over broken denticle.

3. Right element (USNM 498980), all views X200. 3a. oblique oral-inner lateral view, 3b. oral view, 3c. aboral view, 3d. oblique oral-outer lateral view, 3e. outer lateral view, 3f. inner lateral view.

4. Right element (USNM 498981), all views X190, except as noted. 4a. outer lateral view, 4b. inner lateral view, 4c. oblique oral-inner lateral view, 4d. aboral view, 4e. enlargement (X530) showing striae on cusp, 4f. oblique anterior-oral view

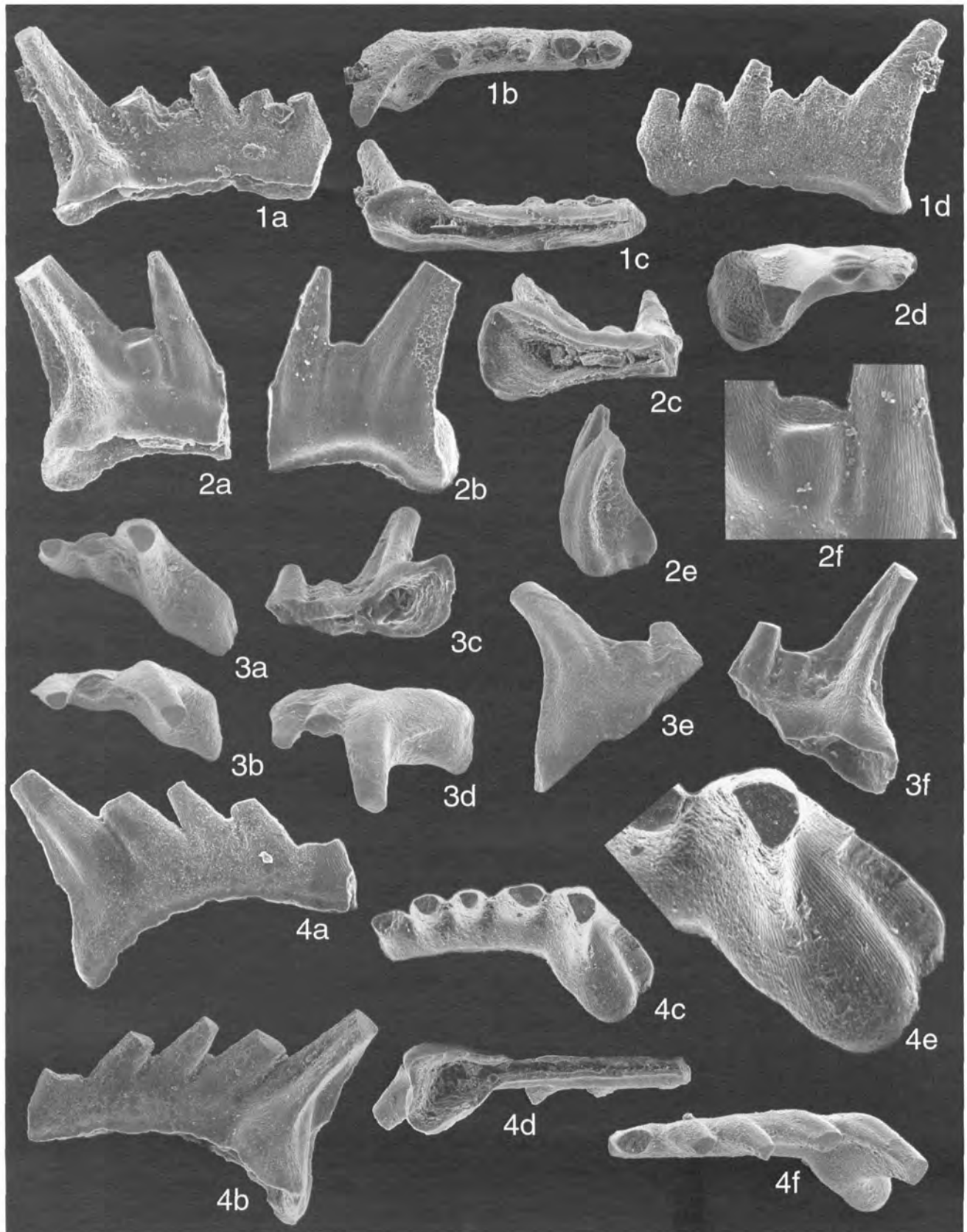


PLATE 17
Iapetognathus landingi new species
Sd element

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959; Seo and Ethington, 1993) All figures X120, except as noted.

1. Left element (USNM 498982) 1a. inner lateral view, 1b. outer lateral view, 1c. posterior view, 1d. aboral view, 1e. oral view.
2. Left element (USNM 498983). 2a. inner lateral view, 2b. outer lateral view, 2c. oblique inner lateral view, 2d. oral view, 2e. aboral view.
3. Left element (USNM 498984), all views X130. 3a. inner lateral view, 3b. outer lateral view, 3c. aboral view, 3d. oral view, 3e. oblique oral-inner lateral view, 3f. posterior view, 3g. anterior view, 3h. oblique posterior-inner lateral view.
4. Right element (USNM 498985). 4a. oblique oral-posterior view, 4b. aboral view, 4c. oral view, 4d. outer lateral view, 4e. inner lateral view.

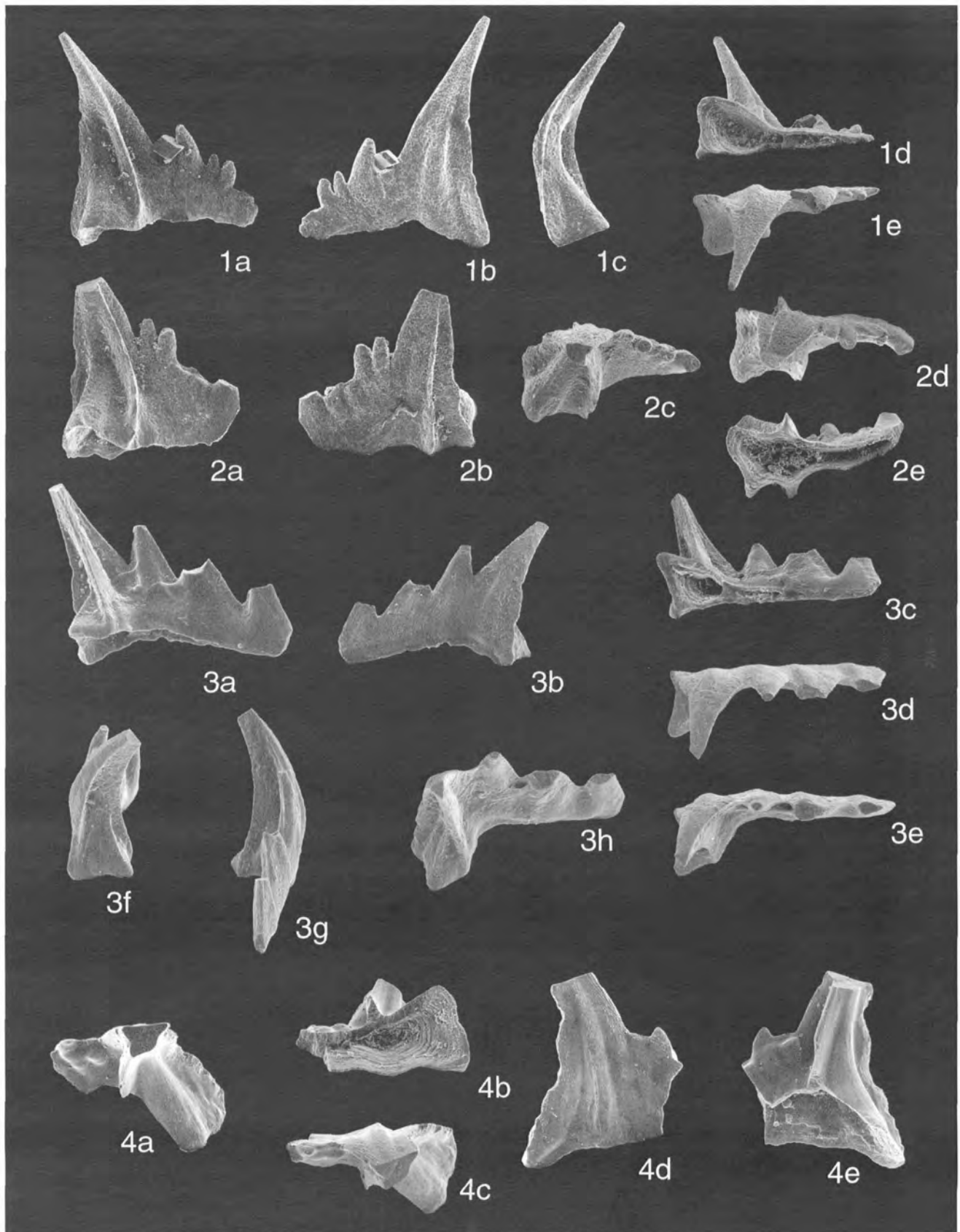


PLATE 18

Iapetognathus landingi new species

Xa element

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959; Seo and Ethington, 1993).

1. Right element (USNM 498986), all views X120. 1a. outer lateral view, 1b. oblique oral-inner lateral view, 1c. oral view, 1d. aboral view, 1e. inner lateral view. Note that the anterior 3 blade denticles broke when turning the element for photography after views 1d and 1e.

2. Right element (USNM 498987), all views X140. 2a. inner lateral view, 2b. outer lateral view, 2c. oral view, 2d. oblique oral view, 2e. aboral view.

3. Left element (USNM 498988), all views X150. 3a. outer lateral view, 3b. posterior view, 3c. aboral view, 3d. oral view, 3e. inner lateral view.

4. Left element (USNM 498989), all views X150, except as noted. 4a. aboral view, 4b. inner lateral view, 4c. posterior view, 4d. outer lateral view, 4e. enlargement (X630) of anterior view.

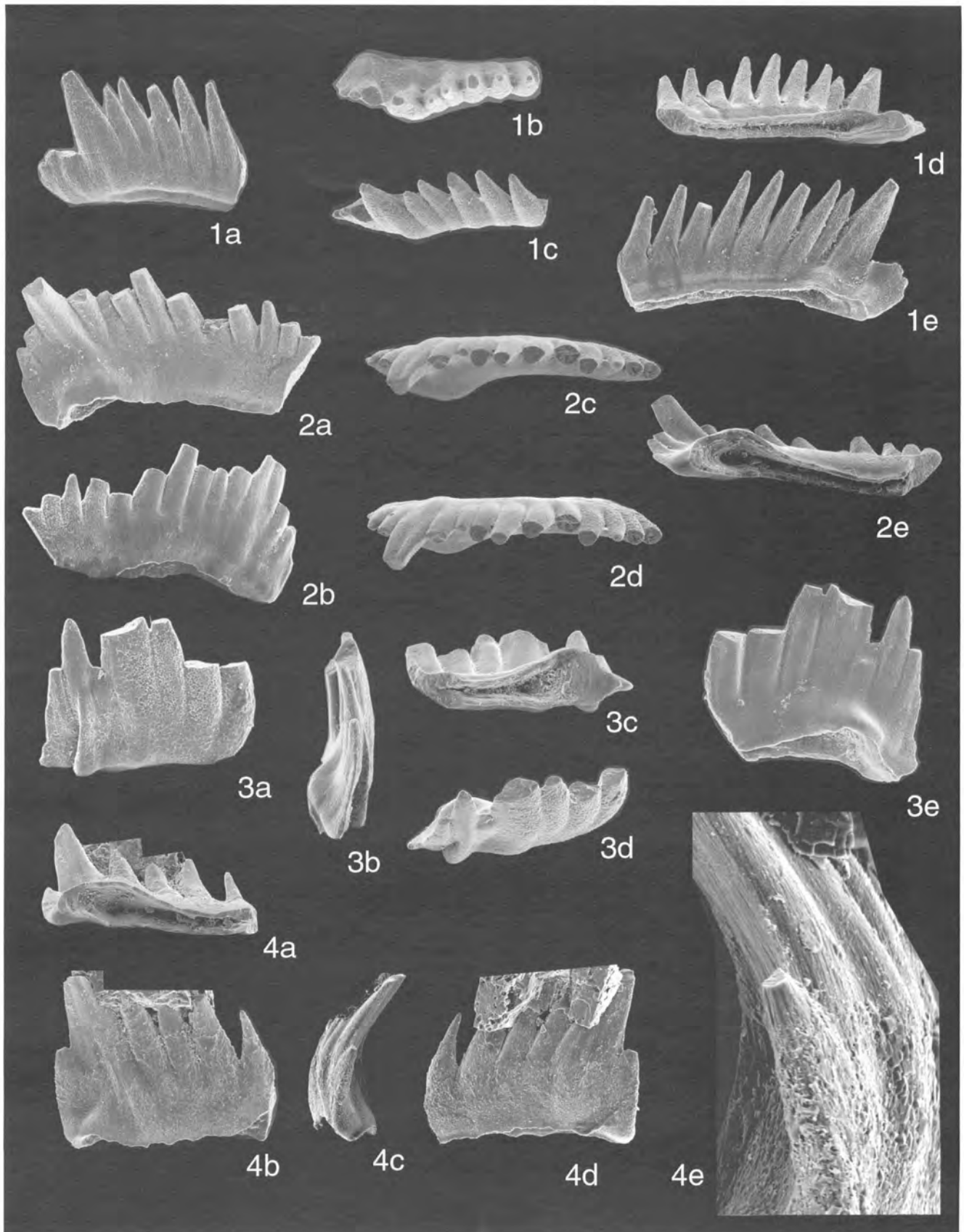


PLATE 19

Iapetognathus landingi new species
Xb and Pb elements

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959, Seo and Ethington, 1993). All figures X150, except as noted.

1. Right Xb element (USNM 498990). 1a. oblique outer lateral view, 1b. outer lateral view, 1c. inner lateral view, 1d. anterior view, 1e. posterior view, 1f. aboral view.
2. Right Xb element (USNM 498991). 2a. outer lateral view, 2b. inner lateral view, 2c. oral view, 2d. aboral view, 2e. enlargement (X500) showing striae on outer side of denticles.
3. Right Pb element (USNM 498992), all views X140. 3a. inner lateral view, 3b. outer lateral view, 3c. oral view, 3d. aboral view, 3e. oblique oral-outer lateral view.
4. Left Pb element (USNM 498993). 4a. aboral view, 4b. inner lateral view, 4c. oral view, 4d. outer lateral view, 4e. oblique oral-posterior view, 4f. enlargement (X630) of oral view showing bifurcation of the posterior margin.

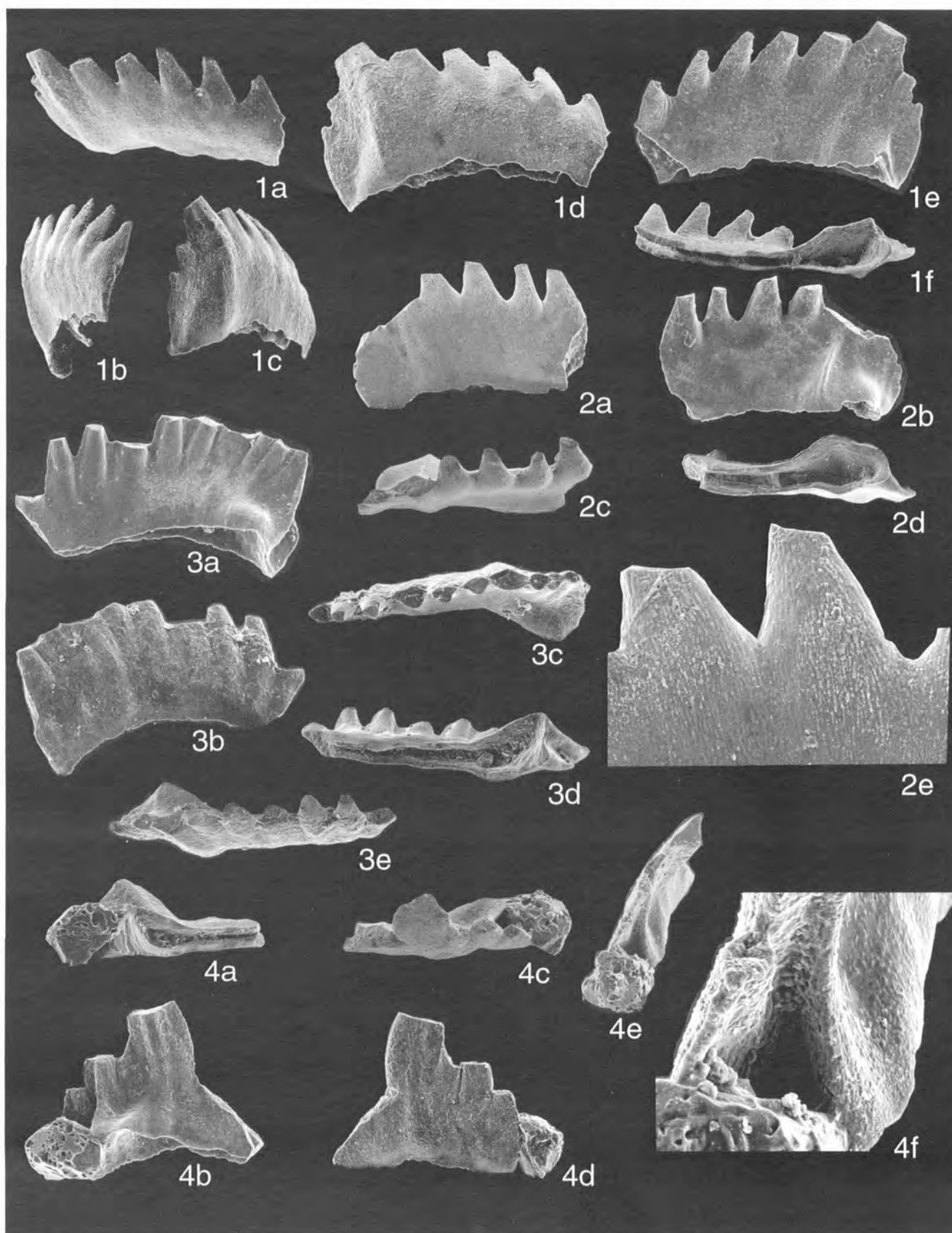


PLATE 20

Iapetognathus landingi new species
Pa element

Specimens are from Bed 6 of the Manitou Formation, Missouri Gulch Section, Colorado (Berg and Ross, 1959; Seo and Ethington, 1993). All figures X150, except as noted.

1. Left element (USNM 498994), all views X130. 1a. inner lateral view, 1b. outer lateral view, 1c. oral view, 1d. aboral view, 1e. anterior view, 1f. posterior view.
2. Right element (USNM 498995), all views X140. 2a. outer lateral view, 2b. inner lateral view, 2c. aboral view, 2d. oral view, 2e. posterior view, 2f. anterior view.
3. Left element (USNM 498996). 3a. inner lateral view, 3b. outer lateral view, 3c. oral view, 3d. aboral view, 3e. oblique oral-outer lateral view, 3f. oblique posterior-inner lateral view, 3g. posterior view, 3h. anterior view.
4. Right element (USNM 498997). 4a. aboral view, 4b. oral view, 4c. oblique posterior-inner lateral view, 4d. outer lateral view, 4e. inner lateral view, 4f. enlargement (X300) showing fine striae extending nearly to the basal margin.

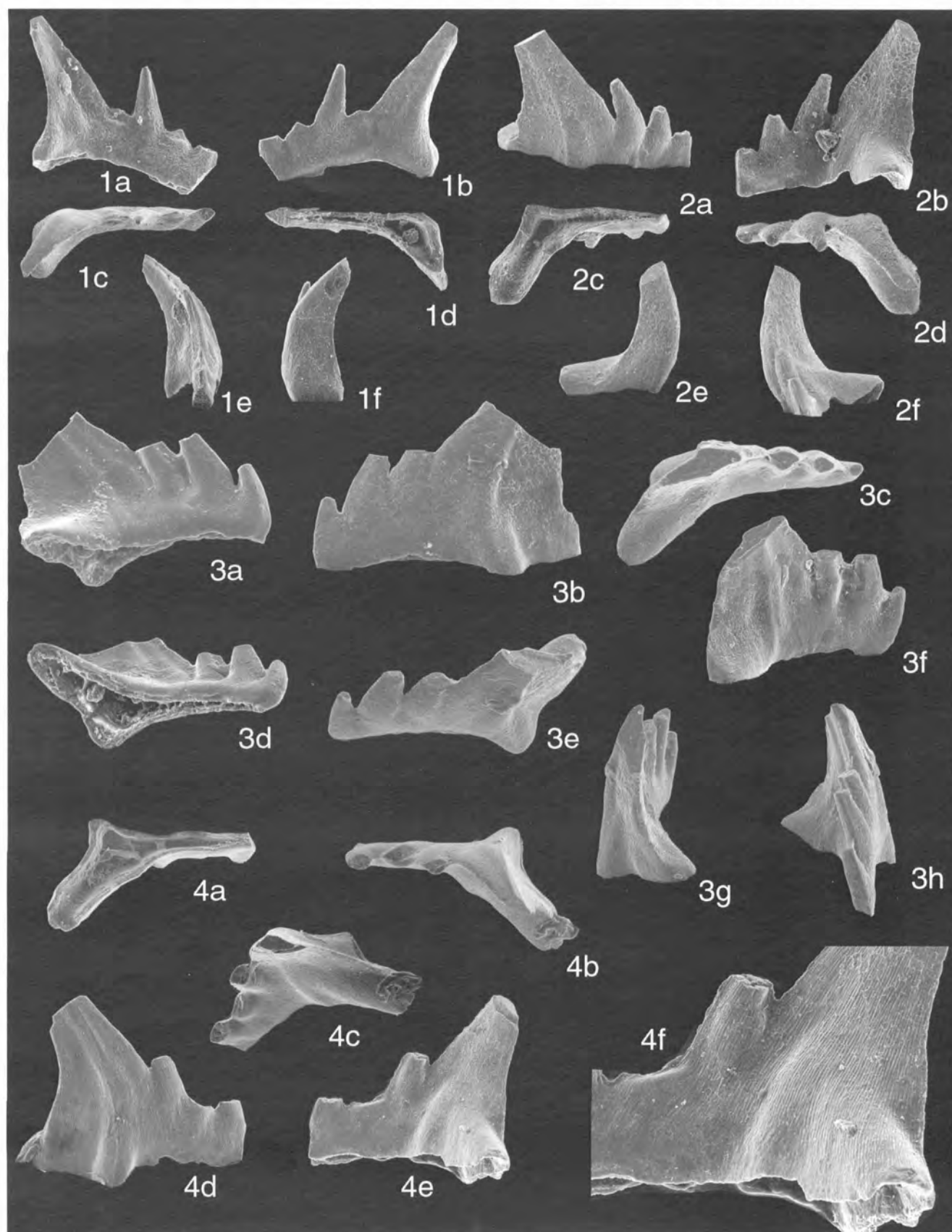


PLATE 21

Iapetognathus sprakersi Landing
Sc, Sb and Sd elements

Specimens from sample TC-1404 in the Wilberns Formation, Threadgill Creek Section, Llano Uplift, Texas, U.S.A. (Miller and others, 1982; Miller and Stitt, 1995).

1. Left Sc element (USNM 498998), all views X140. 1a. oblique anterior-oral view, 1b. oblique oral-inner lateral view, 1c. inner lateral view, 1d. posterior view.
2. Left Sc element (USNM 498999), all views X120. 2a. oblique anterior-oral view, 2b. oblique oral-inner lateral view, 2c. inner lateral view, 2d. posterior view, 2e. oral view, 2f. oblique posterior-outer lateral view, 2g. inner lateral view, 2h. outer lateral view.
3. Left Sc element (USNM 499000), all views X120. 3a. oblique anterior-oral view, 3b. oblique posterior-outer lateral view, 3c. oblique oral-posterior view, 3d. outer lateral view, 3f. basal view.
4. Right Sb element (USNM 499001), all views X115. 4a. oblique basal-outer lateral view, 4b. basal view, 4c. outer lateral view, 4d. oblique posterior-outer lateral view, 4e. oblique oral-outer lateral view.
5. Right Sd element (USNM 499002), all views X115. 5a. oblique oral-outer lateral view, 5b. oral view, 5c. oblique posterior-outer lateral view, 5d. oblique outer lateral view, 5e. outer lateral view.

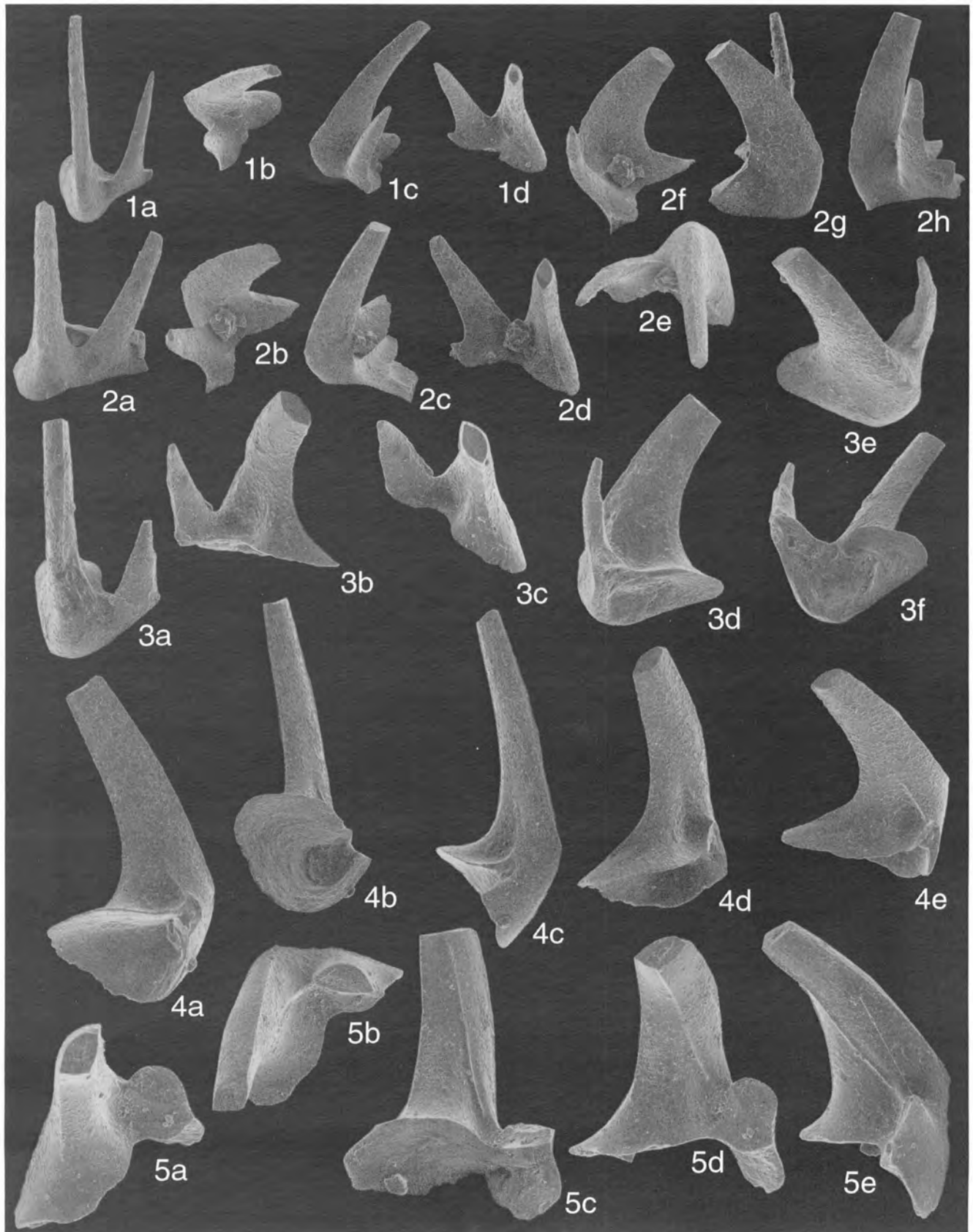


PLATE 22

Iapetonudus ibexensis new genus, new species
Sc and Sb elements

Specimens are from the Lawson Cove section, Ibex area, Utah, U.S.A. described by Miller (1995). The specimens in figures 1 and 4 are from the 438 foot level and the specimens in figures 2 and 3 are from the 435 foot level.

1. Left Sc element (USNM 499003), all views X180. 1a. oral view, 1b. posterior view, 1c. aboral view, 1d. outer lateral view, 1e. anterior view, 1f. inner lateral view.

2. Left Sc element (USNM 499004), all views X190. 2a. aboral view, 2b. oral view, 2c. oblique oral-anterior view, 2d. inner lateral view, 2e. anterior view, 2f. outer lateral view.

3. Left Sb element (USNM 499005), all views X180. 3a. oblique anterior-oral view, 3b. aboral view, 3c. inner lateral view, 3d. anterior view, 3e. outer lateral view, 3f. oral view.

4. Left Sb element (USNM 499006), all views X200. 4a. oral view, 4b. aboral view, 4c. oblique posterior-outer lateral view, 4d. outer lateral view, 4e. posterior view, 4f. inner lateral view, 4g. anterior view.

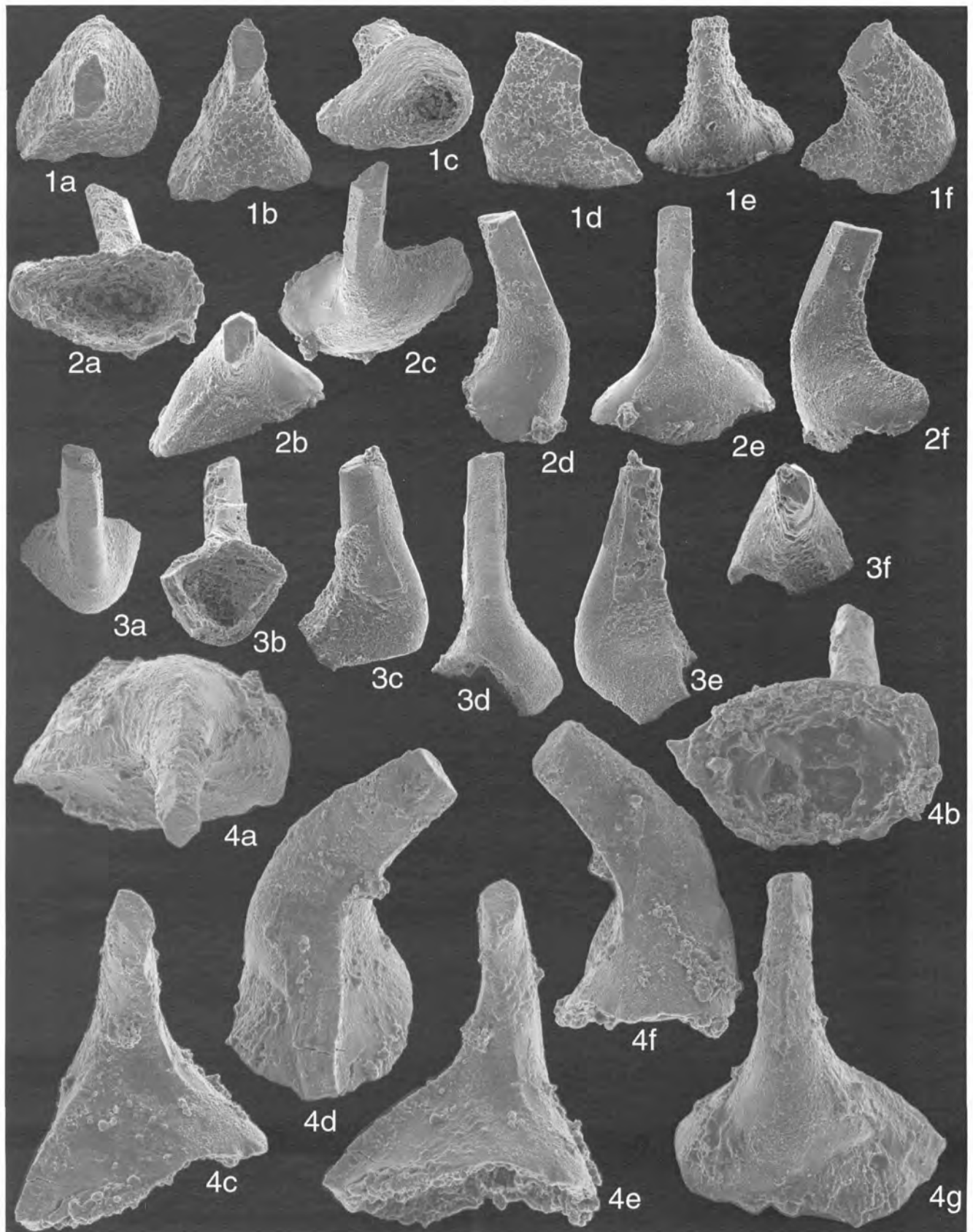


PLATE 23

Iapetonodus ibexensis new genus, new species
Sd and Pa elements

Specimens are from the Lawson Cove section, Ibex area, Utah, U.S.A. described by Miller (1995). The specimens in figures 1 and 3 are from the 435 foot level and the specimens in figure 2 is from the 438 foot level.

1. Right Sd element (USNM 499007), all views X220. 1a. aboral view, 1b. oral view, 1c. posterior view, 1d. inner lateral view, 1e. anterior view, 1f. outer lateral view.

2. Left Sd element (USNM 499008), all views X190. 2a. aboral view, 2b. oblique oral-posterior view, 2c. oral view, 2d. posterior view, 2e. oblique posterior-outer lateral view, 2f. outer lateral view, 2g. anterior view, 2h. inner lateral view.

3. Right Pa element (USNM 499009), all views X200. 3a. aboral view, 3b. oral view, 3c. oblique outer lateral view, 3d. posterior view, 3e. inner lateral view, 3f. anterior view, 3g. outer lateral view.

