

CLASSIFICATION OF THE TRILOBITE SUBFAMILIES HYSTRICURINAE AND
HINTZECURINAE SUBFAM. NOV., WITH NEW GENERA FROM THE LOWER
ORDOVICIAN (IBEXIAN) OF IDAHO AND UTAH

JONATHAN M. ADRAIN, DONG-CHAN LEE, STEPHEN R. WESTROP, BRIAN D.E. CHATTERTON
AND ED LANDING

Adrain, J.M., Lee, D.-C., Westrop, S.R., Chatterton, B.D.E. & Landing, E. 2003 05 20:
Classification of the trilobite subfamilies Hystricurinae and Hintzecurinae subfam. nov.,
with new genera from the Lower Ordovician (Ibexian) of Idaho and Utah. *Memoirs of the
Queensland Museum* **48**(2): 553-586. Brisbane. ISSN 0079-8835.

The Hystricuridae, previously regarded by most workers as a paraphyletic group, is considered on the basis of new and revised silicified species from Utah and Nevada. Major subgroups of hystricurids appear to be monophyletic, but the sister group relationships of several related families require investigation. The Hystricurinae is restricted to *Hystricurus* Raymond, 1913, *Tersella* Petrunina, 1973, and *Flectihystricurus* gen. nov. (type species: *Hystricurus flectimembrus* Ross, 1951). A new subfamily Hintzecurinae is diagnosed. The subfamily appears to be restricted to the upper Skullrockian Stage, and comprises the new genera *Hintzecurus* (t.s.: *Hystricurus paragenalatus* Ross, 1951), *Genalaticurus* (t.s.: *Hystricurus genalatus* Ross, 1951), *Ibexicurus* (t.s.: *I. parsonsi* sp. nov.), *Lavadamia* (t.s.: *L. joplinae* sp. nov.), *Politicurus* (t.s.: *Hystricurus politus* Ross, 1951), and *Rossicurus* (t.s.: *Hystricurus lepidus* Hintze, 1953). □ Trilobites, Hystricuridae, Ordovician, Idaho, Utah.

Jonathan M. Adrain, Department of Geoscience, University of Iowa, 121 Trowbridge Hall, Iowa City, Iowa 52242, USA; Dong-Chan Lee and Brian D.E. Chatterton, Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada; Stephen R. Westrop, Oklahoma Museum of Natural History and School of Geology & Geophysics, University of Oklahoma, Norman, Oklahoma 73019, USA; and Ed Landing, Center for Stratigraphy and Paleontology, New York State Museum, The State Education Department, Albany, New York 12230, USA; received 10 September 2002.

The Hystricuridae has long been considered a grade group of trilobites from which other elements of the Order Proetida Fortey & Owens, 1975, were derived. Although some speculation has been offered (e.g., Fortey and Owens, 1975), there have been no explicit attempts to demonstrate analytically that particular hystricurids are sister taxa of particular derived families and that Hystricuridae is hence paraphyletic. Obstacles to progress have included the generally very poor knowledge we have of most hystricurid species and relatively sparse sampling of the Skullrockian and Stairsian interval of the Lower Ordovician. Silicified faunas from the Great Basin offer the potential for nearly complete knowledge of many species, including a great number of undescribed hystricurid taxa.

The House Formation is the lowest Ordovician rock unit in western Utah and eastern Nevada. It is well exposed and abundantly fossiliferous in its type area, the Ibex region of western Utah (Fig 1A). Trilobites from the formation were described by Hintze (1953), and coeval faunas from the Garden City Formation in Utah (Fig. 1B) were described by Ross (1951). J.M.A. and

S.R.W. are engaged in a comprehensive, field-based study of the Lower Ordovician (Ibexian) faunas of Ross (1951) and Hintze (1953), the first result of which was revision of some dimero-pygids from the upper Fillmore and Wahwah formations (Adrain et al., 2001). We continue the revision here with the description of the Hintzecurinae subfam. nov. comprising 6 new hystricurid genera from the upper House Formation and the equivalent part of the Garden City Formation, together with a new genus of the nominate subfamily.

The new material recovered from the Ibexian of the Great Basin will require many publications to describe fully, and a monograph is in progress on the hystricurids of the House Formation and Garden City Formation equivalent. It is desirable that new genus names necessary to accommodate the hystricurids be made available, in order to facilitate analysis of Skullrockian biostratigraphy and evolutionary patterns, and so that they may be included in the compilation by Jell & Adrain (this volume). To recognise the Hintzecurinae, it is important that the status and content of *Hystricurus* and the nominate Hystricurinae be

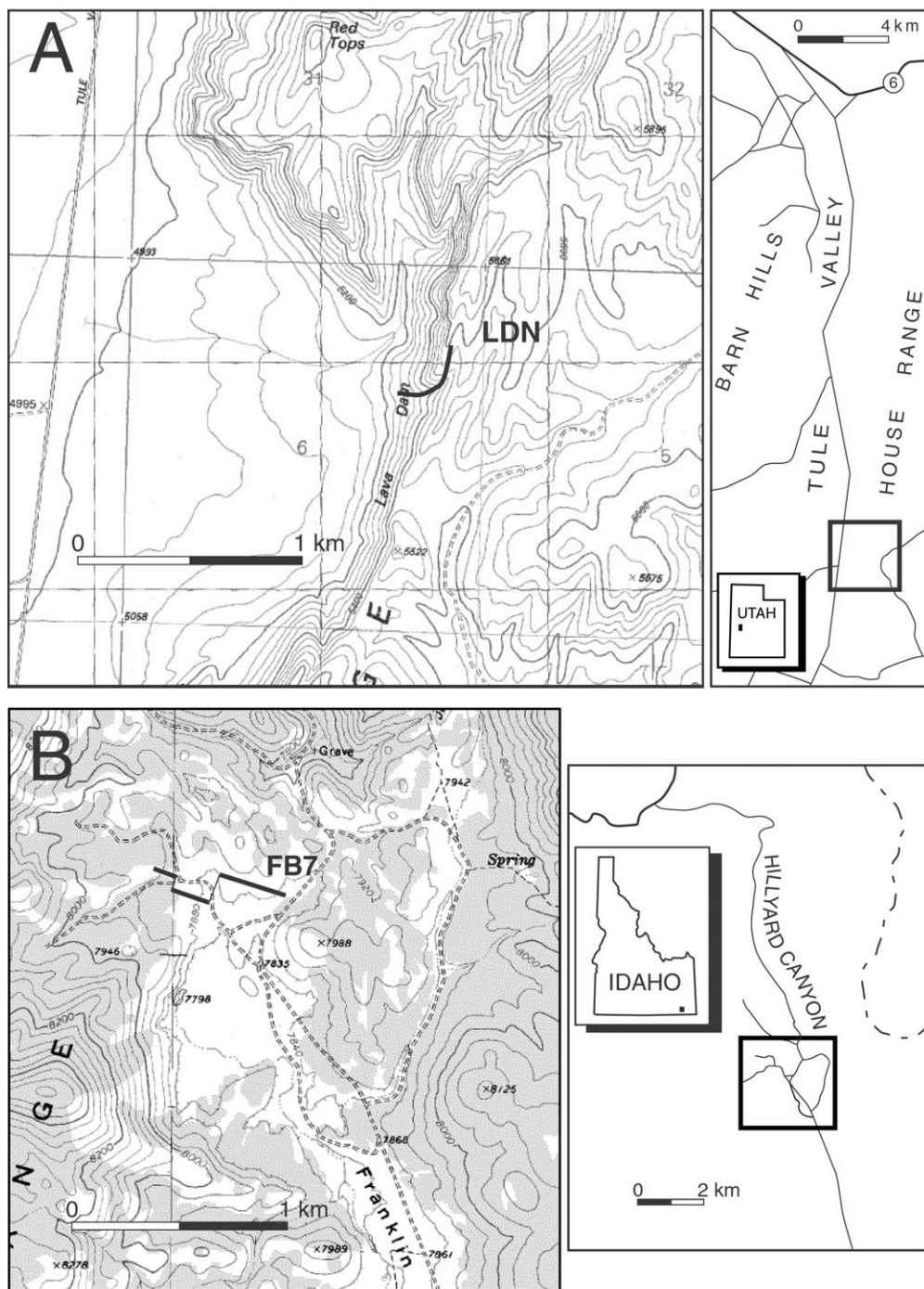


FIG. 1. A, location and line of section Lava Dam North (LDN), Ibex area, southern House Range, Millard County, western Utah. B, location and line of section Franklin Basin 7 (FB7; Locality 7 of Ross, 1951), Bear River Range, Franklin County, southeastern Idaho.

clarified. We refigure the holotype of the type species of *Hystricurus*, illustrate some other members of the genus recovered from the Ibexian of the Great Basin, and erect *Flectihystricurus*. Subsequent publications will describe additional species of the genera erected herein (referred to in remarks on each taxon below) and will treat the remainder of the family.

STRATIGRAPHIC AND BIOSTRATIGRAPHIC BACKGROUND

The lithostratigraphical nomenclature of the Lower and Middle Ordovician succession in western Utah was established by Hintze (1951). The Pogonip Group was a broadly applied term for the package of strata between the distinctive regional marker units of the Dunderberg Formation (Upper Cambrian, Steptoean) and the Eureka Quartzite (upper Whiterockian to Mohawkian). In modern stratigraphic usage, the group is recognized as Lower and Middle Ordovician. In the Eureka district, east-central Nevada (Nolan et al., 1956), the group overlies the Upper Cambrian Windfall Formation, and comprises in ascending order the Goodwin, Ninemile, and Antelope Valley Formations. Hintze (1951) recognised the Pogonip Group in western Utah and easternmost Nevada as overlying the Upper Cambrian Notch Peak Formation (Walcott, 1908; see Hintze et al., 1988) and comprising in ascending order his new House, Fillmore, Wahwah, Juab, Kanosh, and Lehman Formations.

The type section of the House Formation is Hintze's (1951, 1953) Section A in the central House Range of the Ibex area. Other important sections reported on by Hintze (1953) include his Section B and basal Section C (southern House Range) and Section E (Middle Mountain, to the west of Crystal Peak and immediately northwest of the Wah Wah Mountains). Other sections including part or all of the House Formation that have received substantial study include Lava Dam Five (Hintze et al., 1988) and Lava Dam North (Hintze, 1973) in the southern House Range, Lawson Cove (Miller et al., 2001) in the northern Wah Wah Mountains, and a section in the northwestern Drum Mountains (Miller et al., 2001). Miller et al. (2001) divided the formation into three members, in ascending order, the Barn Canyon, Burnout Canyon, and Red Canyon Members (Fig. 2).

Two prominent units within the House Formation form useful regional marker beds. The massive upper bed of the formation lies

immediately above a characteristic articulate brachiopod coquina that is also rich in sclerites of trilobites presently assigned to *Paraplethopeltis* (Hintze's [1953] Zone C, and Ross et al.'s [1997] '*Paraplethopeltis* Zone'). The upper bed is clearly distinguished in steeper cliff-forming sections, and the contact with the overlying and lithologically similar Fillmore Formation is drawn at the point at which the rocks become slope-forming. This physiographic expression can vary, however. In sections along Middle Mountain, the lowest beds of the Fillmore are more resistant than in the southern House Range and form additional small cliffs rather than a slope. A second regional marker is the cliff-forming Burnout Canyon (middle) Member of the House Formation. This 15-20m thick unit is heavily chertified and forms a characteristic rusty brown cliff throughout the Ibex area. Hintze (1951, 1953) referred to it as the 'brown marker bed'.

There are few lithological criteria separating the Barn Canyon Member of the House Formation from the underlying Lava Dam Member of the Notch Peak Formation. The boundary has been drawn on physiographic evidence, namely a break in slope from the cliff-forming Notch Peak to the ledge-and-slope forming House, and also on the upper extent of stromatolitic units common in the Lava Dam Member. Miller et al. (2001) noted that development of stromatolites is often laterally discontinuous and shows significant regional variation. They instead defined the base of the House Formation on the occurrence, said to be geographically widespread, of a coquina formed of sclerites of the trilobite *Symphysurina*. This significantly extends the stratigraphic range of the House Formation, as this boundary is 40m lower than that of Hintze et al. (1988; Miller et al., 2001).

With this redefined boundary, the base of the House Formation corresponds nearly exactly to the base of the *Symphysurina brevispicata* Subzone, according to the trilobite identifications of Loch et al. (1999). In current trilobite biostratigraphy, the '*Symphysurina* Zone' of Ross et al. (1997) extends through the Burnout Canyon Member (although identifiable fossils are sparse in these rocks). The Red Canyon Member includes the '*Bellefontia-Xenostegium* Zone' ('*Bellefontia* Zone' of Miller et al., 2001, fig. 1) and, near its top, the '*Paraplethopeltis* Zone'. The base of the '*Leiostegium-Kainella* Zone' of the overlying Stairsian Stage is drawn at the base of the uppermost massive bed of the

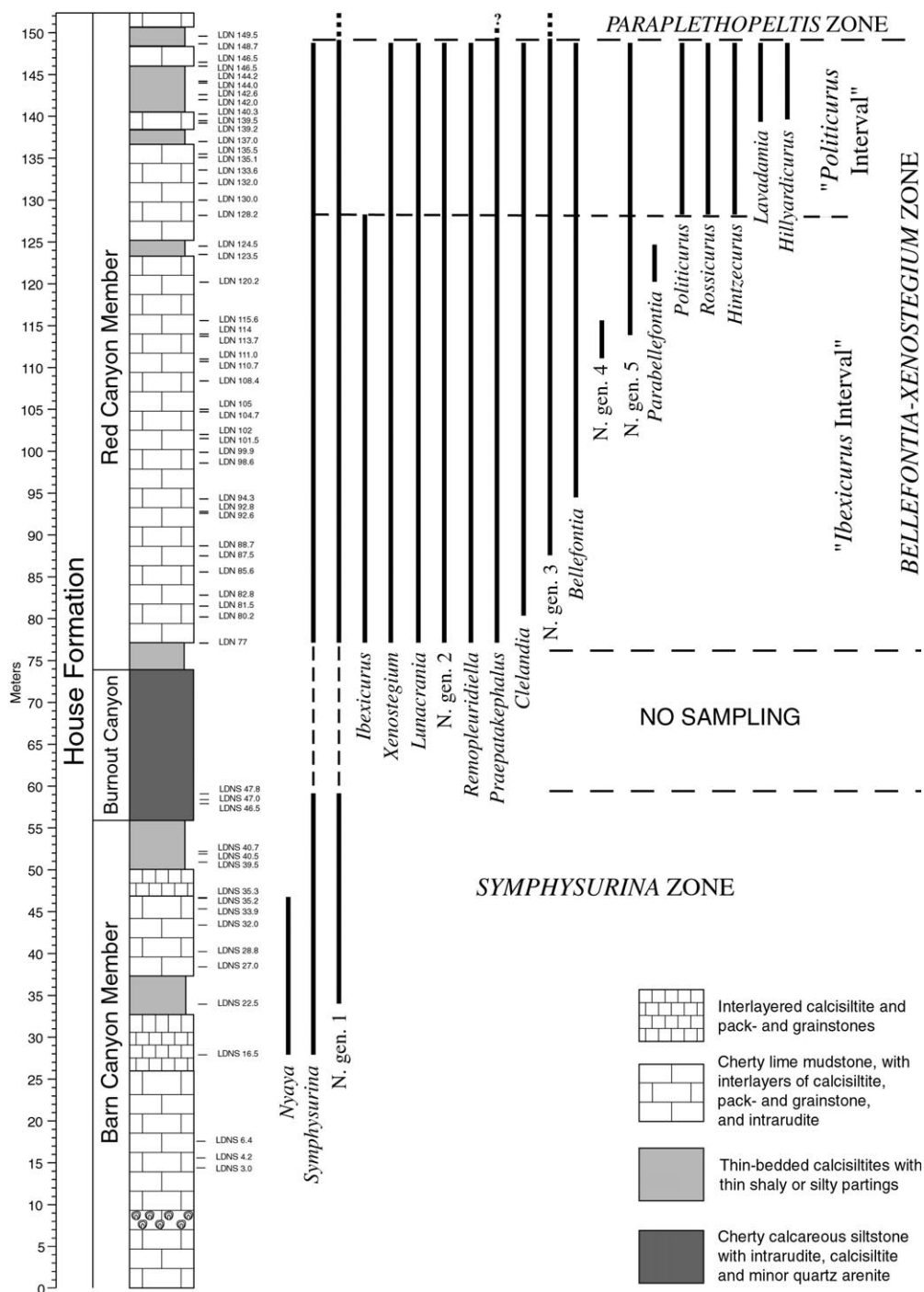


FIG. 2. Sampling horizons and trilobite genus ranges in the House Formation, section Lava Dam North (see Fig. 1). The ranges of all recovered taxa are depicted, including the six new genera described herein plus a further five unnamed genera (N. gen 1-5).

House Formation. The candidate for the global Cambrian-Ordovician boundary datum, the first appearance of '*Iapetognathus* sp. nov. 1' occurs within the '*Symphysurina* Zone', near the base of the *Symphysurina bulbosa* Subzone (Loch et al., 1999; Miller et al., 2001).

Miller (1969) documented the conodont succession of the upper Notch Peak and lower House Formations and Ethington (1978) and Ethington & Clark (1981) treated the conodonts of the House Formation. Popov et al. (2002) described inarticulate brachiopods from the boundary interval. Despite generally good knowledge of House Formation biostratigraphy, the most common macrofaunal elements - trilobites - remain extremely poorly known. No photographic illustrations or systematic revisions of House Formation trilobites have appeared since Hintze (1953). Trilobite biostratigraphy of the boundary interval has been discussed only on the basis of unverified identifications in faunal lists and species range charts (Ross et al., 1997; Loch et al., 1999; Miller et al., 2001), and these have been concentrated mostly on the Cambrian-Ordovician boundary.

Similarly the only published illustrations of trilobites from the Skullrockian part of the Garden City Formation since Ross (1951) are of material from the Cambro-Ordovician boundary interval at Ross's Locality 7 (FB7 of this paper) by Taylor & Landing (1982, text-fig. 5).

Both regions, and in particular the House Formation in the Ibex area, contain some of the richest and best preserved silicified trilobite faunas in the world. The Skullrockian faunas are dominated by hystricurids, *Symphysurina* and asaphids, with less common remopleuridids, missisquoiids, and *Clelandia*. In this paper, we begin a full revision of the hystricurids from the Skullrockian of the Ibex area and Bear River Range. Ross (1951) and Hintze (1953) together formally named only five species of Skullrockian hystricurids: *Hystricurus millardensis* Hintze, 1953, from the Barn Canyon Member, *Hystricurus genalatus*, *H. paragenalatus* and *H. politus* (all Ross, 1951) from the lower Garden City Formation and *H. lepidus* Hintze, 1953, from the Red Canyon Member. All of Ross's species also occur in the Red Canyon Member in the Ibex area. New field sampling has revealed at least 32 new hystricurid species from the Skullrockian part of these sections.

Of these previously named species, a pygidium was confidently assigned only for *H. millard-*

ensis. *Hystricurus lepidus* was based on a cranidium and two librigenae. The librigenae are not congeneric with the cranidium (see below) and hence the species has until now been known from a single specimen.

MATERIALS AND METHODS

REPOSITORY. All illustrated material is housed in the Paleontology Repository, Department of Geoscience, University of Iowa, with specimen number prefix SUI.

ABBREVIATIONS. Sag. = sagittally; exsag. = exsagittally; tr. = transverse.

SAMPLING. *Garden City Formation.* We have remeasured and recollected sections at Ross's (1951) localities 5 (east side of Hillyard Canyon; our HC5), 6 (west side of Hillyard Canyon; our HC6) and 7 (Franklin Basin, just south of Hillyard Canyon; our FB7) in the Bear River Range of southeastern Idaho. New section measurements at all three localities begin at the contact between the St. Charles Formation and the Garden City Formation, and are hence directly comparable to the footages above this contact given by Ross (1951). The holotype of *H. genalatus* is from Section HC6 and those of *H. paragenalatus* and *H. politus* are from FB7. Beds yielding silicified fossils are relatively few in the Garden City Formation, at least as compared to the Pogonip Group in the Ibex area. Upper Skullrockian faunas occur at HC6 27.0-31.5m and at FB7 39.2-44.0m, and these intervals are surely the type localities for Ross's Skullrockian species. They are uniform between the sections with all species shared. An upper Skullrockian fauna also occurs at Section HC5 38.1m, but comparison with the undescribed faunal succession in the Ibex area indicates it is older than the HC6/FB7 horizons. It contains undescribed species of *Rossicurus* and *Politicurus*, but appears to have no species in common with HC 6 27.0-31.5 and FB7 39.0-44.2m. Ross (1951) did not report sample sizes. We processed more than 90kg of rock from FB 7 39.2-44.0m. We have not counted trilobite sclerites, but total sample size is on the order of thousands of specimens.

Some material is described from the Stairsian of the Garden City Formation, including specimens from 'Zone E' ('*Tesselacauda* Zone') at Section HC5 106.7m and FB7 102.1m, and from 'Zone F' ('*Rossaspis superciliosa* Zone') at Section HC6 127.5-131.3m.

House Formation. We measured and collected sections in the Ibex area at Lava Dam North (Fig. 2; southern House Range; our LDN and LDNS), the topmost part of Section B (southern House Range, about 3km north of Lava Dam North; our B-TOP), all of Section E (our EEE) at Middle Mountain, and a section through the uppermost House and Fillmore farther to the north on Middle Mountain (our MME). All House Formation material figured herein was collected from section LDN.

At Lava Dam North, it is possible to access the top of the section via a rough jeep track leading from a road running north from the Steamboat Pass road (Fig. 1A). This allowed extensive sampling of silicified fossils. We collected 43 horizons in the type section of the Red Canyon Member at LDN, a mean sampling density of one sample per 1.69m. Sampling is fairly evenly spaced throughout the member (Fig. 2). Only the uppermost sample, LDN 149.5m, failed to yield abundant silicified fossils. This sample is from the brachiopod coquina of the '*Paraplethopeltis* Zone'. Large '*Paraplethopeltis*' sclerites were evident in outcrop, but only fragmentary librigenae were silicified. Fossils in these beds are pervasively silicified at section B-TOP. The other 42 horizons yielded abundant and well preserved silicified trilobites. The amount of rock processed from each horizon ranged from 2.68kg to 34.42kg, with an average of 12.22kg. Full counts of silicified trilobite sclerites have not been made, but numbers per horizon range from dozens in the smallest samples to typically hundreds in most samples, to thousands in the richest samples.

This level of sampling contrasts markedly with that which Hintze (1953) was able to carry out. Hintze reported collections from 15 trilobite-bearing House Formation horizons at Section E, 11 from Section B, and 9 from Section A. This is a stratigraphic sampling density about 15-25 % as intense as ours (we collected 57 trilobite-bearing horizons in total at LDN and LDNS). Taking into account the probable contrasts in individual sample sizes (Adrain et al., 2001: 947-948), overall sampling intensity in the present study may be conservatively estimated as at least a 40-fold increase over that on which the Ross et al. (1997) biostratigraphy was based.

Our line of section at LDN is not identical to Hintze's (1973; followed by Miller et al., 2001). The lower part of Hintze's section proceeds up a slope to the north of a prominent gully leading to the upper part of the section. This line of section

was evidently chosen for posterity, so that the painted numbers left by Hintze (1973) would be available for future investigators. A section within the gully, by contrast, is much more subject to change through flash flooding and storm runoff. However, it is also much more fully exposed than the section on the slope and is where we chose to measure the bottom part of our section. Our LDN section joins Hintze's (1973) Lava Dam North section in the lower part of the type section of the Red Canyon Member, and the sections are largely coincident from that point on (but see discussion of fault below). Silicified fossils are most easily prospected and collected in slope-and-ledge forming ridge-crest exposures, where beds often weather in bedding plane exposures. The Red Canyon Member in the upper part of LDN is weathered and exposed in this way, but the Barn Canyon Member is more steeply exposed in both the gully of our section and the slope of Hintze's section. However, the upper part of the Barn Canyon Member is well exposed on a ridge crest immediately to the south of LDN, which we measured and collected as Section LDNS. All of our Barn Canyon collections at Lava Dam are from LDNS and all of our Red Canyon collections are from LDN. Figure 2 shows the LDN section, with the position of the LDNS collections in their correlative positions. Bed by bed correlation of the sections is trivial, as they are adjacent and both include the datum of the base of the Burnout Canyon Member. We did not obtain trilobites from the Burnout Canyon Member.

The described type section of the Red Canyon Member (Hintze, 1973; Miller et al., 2001) contains one significant error in the interval of 480-496' of Hintze's measurements. Here Hintze's section runs across a low saddle in the ridge. Miller et al. (2001: 64) described continuous section across this feature: 'Unit is poorly exposed in a low saddle; dip of beds indicates a small syncline in this saddle [486-488]'. In fact, the saddle is a fault block. There is a prominent trilobite-rich bed at 480' at the base of the saddle, which lies just beneath a distinctive brown siltstone bed. The same bed (with an identical fauna) is repeated at 488' on the far side of the saddle. We collected another rich bed at 494' at the end of the saddle, and an extremely rich bed dominated by the asaphid *Parabellefontia* at 496'. These horizons, however, are separated by a fault which terminates the saddle. Section is continuous downslope beneath Hintze's 496' and to the north

of the fault. Here, the rich 480'/488' trilobite bed can be located in exactly the same proximity to the distinctive brown siltstone as at 480' on the far side of the saddle. These beds can therefore be used to correlate across the complex faulted interval. In our measurement, the rich 480'/488' trilobite bed occurs at LDN 113.7m, the siltstone at LDN 114.0m, the 494' trilobite bed is repeated at LDN 115.6m, and the *Parabellefontia* bed (496' in Hintze's measurement) is at LDN 124.5m. Hence, the Hintze & Miller et al. sections repeat 8 feet of section, but omit about 9m (which is faulted out between their 494' and 496'). This is significant because the affected interval is rich in silicified trilobites and contains substantial species turnover.

Fillmore Formation. Although this paper concentrates on hystricurids from the upper House Formation and equivalent, some Stairsian material from the Fillmore Formation is figured to illustrate the basis for the revised diagnosis of the Hystricurinae provided below. We measured and redescribed the lower Fillmore Formation at our Section MME, Middle Mountain (see above) and Hintze's Sections C and G. At MME, the contact between the House and Fillmore Formations is drawn at 8.8m. 'Zone D' ('*Leiostegium-Kainella* Zone') and 'Zone E' ('*Tesselacauda* Zone') are represented at MME by rich silicified faunas. The top of the section (MME 132.0m) is within 'Zone F' ('*Rossaspis superciliosa* Zone'). Section G begins within the lower Fillmore Formation. The lower part of the section has not yielded silicified collections. The first rich horizons encountered, from which some specimens are figured herein, are at G 26.6m and 27.0m. These faunas are not easily assigned to either 'Zone E' or 'Zone F' and are in a stratigraphically intermediate position between them. They are similar in generic composition to both but share few or no species with either zone. This interval awaits proper biostratigraphic zonation once the faunas are more fully described. A rich horizon at G 48.5m is within 'Zone F' ('*Rossaspis superciliosa* Zone').

SYSTEMATIC PALAEONTOLOGY

Family HYSTRICURIDAE Hupé, 1953

INCLUDED GENERA. *Amblycranium* Ross, 1951; *Etheridgaspis* Kobayashi, 1940; *Flectihystricurus* gen. nov.; *Genalaticurus* gen. nov.; *Glabretina* Lochman, 1965; *Guizhouhystricurus* Yin in Yin & Li, 1978; *Hillyardina* Ross, 1951 (= *Metabowmania*

Kobayashi, 1955); *Hintzecurus* gen. nov.; *Hystricurus* Raymond, 1913 (= *Vermilionites* Kobayashi, 1955); *Hyperbolochilus* Ross, 1951; *Ibexicurus* gen. nov.; *Lavadamia* gen. nov.; *Nyaya* Rozova, 1963; *Omuliovia* Chugaeva, 1962; *Pachyocranium* Ross, 1951; *Paenebeltella* Ross, 1951; *Parahystricurus* Ross, 1951; *Paraplethopeltis* Bridge & Cloud, 1947; *Politicurus* gen. nov.; ?*Psalikilopsis* Ross, 1953; ?*Psalikilus* Ross, 1951; *Rollia* Cullison, 1944; *Rossicurus* gen. nov.; *Tanybregma* Jell & Stait, 1985a; *Tasmanaspis* Kobayashi, 1940; *Tersella* Petrunina, 1973.

EXCLUDED OR QUERIED GENERA. *Natmus* Jell, 1985, from the Digger Island Formation of Victoria is an exceedingly micropygous trilobite with a cephalic caecal sculpture of raised, anastomosing lines, prominent pits in the anterior border furrow, and a pustulose swelling in the preglabellar field in some specimens. It was one of the examples used by Fortey & Hughes (1998) in their argument that the preglabellar swelling represented a brood pouch. In this view, Jell's (1985) species *N. victus* and *N. tuberus* are potential sexual dimorphs of a single species. *Natmus* is similar in many respects to Late Cambrian *Crucicephalus ocellatus* Shergold, 1972, and Early Ordovician *Amzasskiella* Poletaeva in Khalfin, 1960 (= *Triplacephalus* Lu & Qian in Zhou et al., 1977, fide Peng, 1984). All have very similar, eulomid-like, glabellar furrows, strong caecal sculpture on the cephalic pleurae, extremely strong eye ridges, anterior border furrow pits, preglabellar 'brood pouch' swelling in at least some specimens, and many thoracic segments with a minute pygidium. *Natmus* differs from the other taxa mainly in that its pleural lobes are not extremely broad and 'olenimorph' (sensu Fortey & Owens, 1990). Jell (1985) noted that there were no obvious comparisons of *Natmus* within the hystricurids, beyond a general resemblance to *Psalikilus* Ross, 1951. *Psalikilus pikum* Hintze, 1953, is strikingly homeomorphic on *Natmus* in general cranial dimensions, prominent eye ridge, and stalked eye, but lacks the caecal sculpture, preglabellar swelling, anterior border furrow pits, and extremely micropygous condition. Instead it has the conventional tuberculate sculpture and paired cephalic spine array typical of hystricurids. Hence, we regard *Natmus* as unrelated to the hystricurids. Classification of the group to which it belongs requires work. Lu and Qian (in Zhou et al. 1977) erected *Triplacephalidae* for *Amzasskiella*, *Crucicephalus*, and *Triplacephalus*

(since placed in synonymy of *Amzasskiella*), but the broader affinity of this 'family' is uncertain. Peng (1990) placed it in synonymy of Nepeidae Whitehouse, 1939, a group with a rich history in the Middle and Upper Cambrian of Australia (e.g., Öpik, 1967, 1970), an opinion followed by Fortey & Hughes (1998).

Taoyuania Liu in Zhou et al., 1977 (= *Batyraspis* Apollonov & Chugaeva, 1983), fide Lu & Zhou, 1990, Peng, 1990), has been considered a hystricurid, but its affinities are problematic. It is known from the uppermost Cambrian and lower Tremadoc. Cranidia of species of *Taoyuania* achieve a fairly large adult size, with prominent, dense, tuberculate sculpture on the cranidium, a long anterior border, large palpebral lobes, and a slender occipital spine (Peng, 1990, pl. 8, figs 1-9). They certainly bear strong resemblance to hystricurids. Librigenae are unknown. There are problems with a hystricurid affinity, however. Peng (1990: 86) felt that the pygidium of *Taoyuania nobilis* Peng, 1984 (Peng, 1984, pl. 9, fig. 6) 'shows a close relationship to some hystricurid genera on account of the transversely semi-elliptical outline, the short (sag.) axis and the bisected pleurae'. While this is generally true, it also bears prominent and densely spaced terrace lines, subparallel with its margin, distributed across its broad and concave border and onto its pleurae. This morphology is unknown in any hystricurid. Further, the glabella is hour-glass shaped, pinching in opposite the front of the palpebral lobe, then expanding around the frontal lobe. This, too, is unknown in any hystricurid, but is characteristic of leiostegiids. Apollonov and Chugaeva (1983) classified their *Batyraspis*, which we agree is a synonym of *Taoyuania*, in Leiostegiidae. Peng (1990), in arguing for a hystricurid affinity, noted that a prelabellar field is not typical of leiostegiids. The prelabellar field of *Taoyuania* is very short, however, particularly sagittally, and it appears to bear a very weakly developed plectrum (Peng, 1990, pl. 8, figs 1,2,4), indicating a possibly conterminant hypostome (sensu Fortey, 1990). Available evidence is equivocal; *Taoyuania* may prove to be a hystricurid, or it may prove to be a leiostegiid.

Holubaspis Přibyl, 1950, is distributed through the Bohemian lower and upper Tremadoc (see Mergl, 1984, 1994). It has been classified (Vaněk, 1965; Mergl, 1984, 1994) as Hystricuridae, with Vaněk (1965) making comparison with *Psalikilopsis* Ross, 1953. The

genus does not resemble *Psalikilopsis*. The pygidium of *Holubaspis*, misassigned by Vaněk (1965) to *Eulomina* (Mergl, 1984: 37), is very small, with only two axial rings and a narrow pleural area, whereas that of *Psalikilopsis* is large, with four axial rings, a large, vertical 'border', and flange-like pleural processes which merge and project posteriorly as a spine (Ross, 1953, pl. 63, figs 2, 6, 7). The cranidium of *Psalikilopsis* has a distinct prelabellar field, whereas that of *Holubaspis* entirely lacks one. *Holubaspis* does have a tuberculate sculpture on the cranidium and particularly on the librigena (Mergl, 1994, pl. 4, figs 7, 8) that is very similar to that developed by hystricurids. Its vaulted cephalon and librigenal spine, which is nearly lost in the holaspid, is broadly comparable to those of some undescribed taxa from the House Formation, and its hypostome (Mergl, 1984, pl. 4, fig. 10) is strikingly similar to those we have recovered in association with Great Basin hystricurids. Its pygidium, however, is not closely comparable to that of any other hystricurid. *Holubaspis* seems best regarded as a possible hystricurid, but evaluation of its close affinity may require discovery of new data.

Kobayashi (1955) erected a number of genera from the McKay Group of southern British Columbia, Canada, with type species known from sparse (often single specimen) and poorly illustrated material. Potential hystricurids among these include *Gonioteloides*, *Metabowmania* and *Neotaenicephalus*. We agree with Boyce (1989) that *Metabowmania* is a junior synonym of *Hillyardina*. *Neotaenicephalus* is so poorly known (a single very poorly preserved cranidium) that it is impossible to compare with other taxa. We consider it a nomen dubium and restrict it to its type. *Gonioteloides* is problematic. Berg & Ross (1959) illustrated a pygidium assigned to *G. cf. monoceras* Kobayashi, from the Manitou Formation of Colorado, and compared its prominent posterior projection with those of *Psalikilopsis cuspidata* Ross, 1953, and *Psalikilus paraspinosum* Hintze, 1953, which they illustrated (Berg & Ross, 1959, pl. 21, fig. 6) for the first time. Cephalic morphology of *Gonioteloides*, however (Adrain & Westrop, unpubl. data) is not remotely comparable to that of *Psalikilus*. We regard the affinities of *Gonioteloides* as uncertain pending full documentation.

REMARKS. The origin and phylogenetic structure of Bathyruridae is the subject of work in progress by J.M.A. and S.R.W. Of relevance here

is the status of *Omuliovia* and *Etheridgaspis*. Zhou & Fortey (1986) assigned *Omuliovia* Chugaeva, 1962, to the Bathyruridae, noting its close similarity and possible synonymy with the then poorly known *Etheridgaspis* Kobayashi, 1940. The type species of *Etheridgaspis* was revised by Jell & Stait (1985b), who classified the genus as Hystricuridae. They noted similarity with *Omuliovia*, and considered that 'If this similarity has any phylogenetic basis it could be used in support of the suggestions by Fortey and Owens (1975) that the Bathyruridae, where *Omuliovia* is placed, may have evolved from the Hystricuridae'. This implies a monophyletic Bathyruridae and a paraphyletic Hystricuridae. Zhou & Fortey, in contrast, stated 'Fortey and Owens (1975: 229) concluded that some of the bathyrurids may have had their origin in the subfamily Hystricurinae. The transitional characters of *O. granosa* between bathyrurid and some earlier hystricurid forms indicate that *Omuliovia* is most likely one of the bathyrurids which were derived from the hystricurid stock'. This implies a polyphyletic Bathyruridae and a paraphyletic Hystricuridae. This reflects an earlier suggestion by Fortey & Owens (1975: 228-229) that the 'bathyrurines' may have had an independent 'hystricurid' origin than did the 'bathyrurellines'. If this were really the case, then maintaining them together in the Bathyruridae would be unsupportable and they should be classified as separate families. Further, if both *Omuliovia* and *Etheridgaspis* were truly sister taxa to some or all Bathyruridae, they should be classified as such, instead of in a paraphyletic Hystricuridae. We consider, however, that both genera are hystricurids and are not related to Bathyruridae. Based on work in progress and new Ibexian diversity, we regard Bathyruridae as monophyletic. Bathyrurinae and Bathyrurellinae, however, are unlikely to each prove monophyletic as presently conceived.

Hystricurus has been one of the biggest, largely meaningless, taxa of convenience in post-Cambrian trilobite work. The bulk of hystricurid species, most inadequately described, have been assigned to the genus. Reasons for this are twofold. First, most hystricurid species have been very poorly known. Even those described by Ross (1951) and Hintze (1953) have typically not been definitely associated with pygidia or even librigenae and, although well illustrated for their time, much more comprehensive documentation is possible. In general, tuberculate hystricurids have simply been

assigned to *Hystricurus*. A second reason is that the morphology of the type species, *H. conicus* has been obscure, allowing indiscriminate treatment of the genus. *Hystricurus conicus*, like many of Raymond's genera and type species, should not have been designated type species of a new genus. It is based on a single poorly preserved specimen which has previously not been photographically illustrated. However, with the additional material described by Desbiens et al. (1996) and revision of the holotype (see below), its affinity among better known species is clear. The distinctive clade to which it belongs can now be effectively diagnosed, and the concept of its subfamily clarified.

Work in progress on comprehensive revision of all previously named hystricurid species along with an even greater number of new and undescribed taxa from the Pogonip Group and the Garden City Formation facilitates a new classification of the Hystricuridae. Previously almost universally regarded as a paraphyletic group (e.g., Fortey & Owens, 1975; Lee & Chatterton, 1997), it is increasingly clear that hypotheses of phylogenetic relationship are possible and that large components of the hystricurids form putative clades. Outstanding questions involve the origins and sister group relationships of the Dimeropygidae Hupé, 1953, Aulacopleuridae Angelin, 1854, and Bathyruridae Walcott, 1886. These, however, appear largely tractable on the basis of the new information accumulating from our Ibexian field sampling. As a result, we can begin to recognise hystricurid subfamilies whose monophyly can be asserted and tested. Here, we diagnose Hystricurinae and Hintzecurinae. Genera listed above as assigned to Hystricuridae but not listed under either of the subfamilies dealt with below are assignable to new, as yet unnamed, subfamilies and are the subject of works in progress.

Subfamily HYSTRICURINAE Hupé, 1953

INCLUDED GENERA: *Flectihystricurus* gen. nov.; *Hystricurus* Raymond, 1913; *Tersella* Petrunina, 1973.

DIAGNOSIS. Cranidia with very short anterior sections of facial suture; anterior part of cranium relatively narrow and small; very large eyes and large palpebral lobes; glabella 'fiddle-shaped' with anterior, waisted constriction; posterior fixigenae extended prominently in transverse direction; pygidium relatively large,

with at least three fully developed segments, and often prominent posterior pleural spines.

Hystricurus Raymond, 1913

TYPE SPECIES. *Bathyurus conicus* Billings, 1859, from the Beauharnois Formation of Quebec, Canada.

OTHER SPECIES. *Hystricurus deflectus* Heller, 1956; *Hystricurus eos* Kobayashi, 1955; *Hystricurus oculilunatus* Ross, 1951; *Hystricurus* sp. nov. A, herein; *Hystricurus* sp. nov. B, herein.

DIAGNOSIS. Glabella strongly 'fiddle-shaped', with moderate to prominent waisting anteriorly; eye extremely large and palpebral lobe very long; librigenal field narrow and genal spine short; occipital ring and posterior border lacking spinose sculpture; pygidium with 3 or 4 fully defined and tuberculate axial rings, a pair of tubercles or short spines on the terminal piece, and a large spine on the distal part of the posterior pleural band of at least the first segment, which merges into the anterior pleural band of the next most posterior segment; pygidium with prominent smooth vertical 'wall' under pleural spines, and well-developed ventral border bearing lateral terrace lines.

REMARKS. *Hystricurus*, as defined herein, is a highly distinctive clade of Laurentian species. Its sister taxon appears to be *Tersella* Petrunina, 1973, which occurs on the Siberian Platform (type species *T. strobilata* Petrunina, 1973; other species include *Nyaya novozemelica* Burskiy, 1970, *N. paichoica* Burskiy, 1970, *T. (?) magna-oculus* Burskiy, 1970, *T. concinna* Petrunina, 1973, *T. altaica* Petrunina, 1973 and *Hystricurus (?) oculus* Weber, 1948 [Antsygin, 1978]). *Hystricurus sainsburyi* Ross, 1965, should also be assigned to *Tersella*. Ross's fauna, from the Seward Peninsula, Alaska, has strong Siberian affinities and may be derived from an accreted terrane. *Tersella* shares the very strongly waisted glabellar form of *Hystricurus*, the narrow anterior part of the cranium, the large eyes, and the general dimensions of the pygidium. It is distinct, however, in that its frontal area is even more reduced than that of *Hystricurus*, it typically shows a dorsally convex, almost swollen, preglabellar field, its eyes are even larger and its palpebral lobes correspondingly huge, its preglabellar furrow is transverse as opposed to arcuate anteriorly, its pygidium usually lacks spines, and it typically lacks the coarsely tuberculate dorsal sculpture of *Hystricurus*. *Hystricurus* is compared with *Flecthystricurus* gen. nov. below.

The pygidial pleural spines characteristic of *Hystricurus* are, on the evidence of isolated thoracic segments and small pygidia, clearly derived from the distal parts of the posterior pleural bands (this is also the position of the much less prominent spines in *Flecthystricurus*). However, in large specimens, including all of those illustrated in Fig. 4, they are extended posteriorly to effectively straddle the posterior pleural band and the anterior pleural band of the next most posterior segment. The interpleural furrow is interrupted by, deflects slightly posteriorly, and terminates against the spine. This condition is restricted to, and synapomorphic for, *Hystricurus*.

Species of *Hystricurus* from the Pogonip Group and Garden City Formation will be described in detail in a forthcoming work. Some are figured here (Fig. 4) and discussed briefly below to demonstrate the generic concept.

Hystricurus conicus (Billings, 1859) (Fig. 3)

Bathyurus conicus Billings, 1859: 366, fig. 12c.
Hystricurus conicus (Billings); Raymond, 1913: 60, pl. 7, fig. 9.
Hystricurus conicus (Billings); Desbiens et al., 1996: 1146, pl. 3, figs 1-8, 10-12, 15 [with synonymy to date].

MATERIAL AND OCCURRENCE. Holotype, GSC 516, 'Beekmantown Group near Beauharnois, Quebec'; additional material figured by Desbiens et al. (1996), who demonstrated that the species - and the specimen studied by Billings - is from the Ogdensburg Member of the Beauharnois Formation, Beekmantown Group, Montreal area, Quebec, Canada. They considered that the fauna containing *Hystricurus conicus* correlates with the *Strigigenalis caudata* Zone of the Catoche Formation of western Newfoundland (see Boyce, 1989) and with 'Zone G2' of the Great Basin succession.

REMARKS. The holotype has not previously been photographically illustrated. It is unquestionably conspecific with those figured by Desbiens et al. (1996) and demonstrates the short frontal area, glabellar waisting, and very large palpebral lobes shared with the other species (Fig. 4). *H. conicus* is most similar to *H. oculilunatus*, differing most obviously in the much coarser tuberculate sculpture and shorter genal spine.

Hystricurus oculilunatus Ross, 1951 (Fig. 4A,E,I)

Hystricurus oculilunatus Ross, 1951: 47, pl. 10, figs 1-3, 5, 8, 9, 12.
unassigned pygidia from Zone 'F' (not described); Ross, 1951: pl. 17, figs 23, 28, 29 (only).

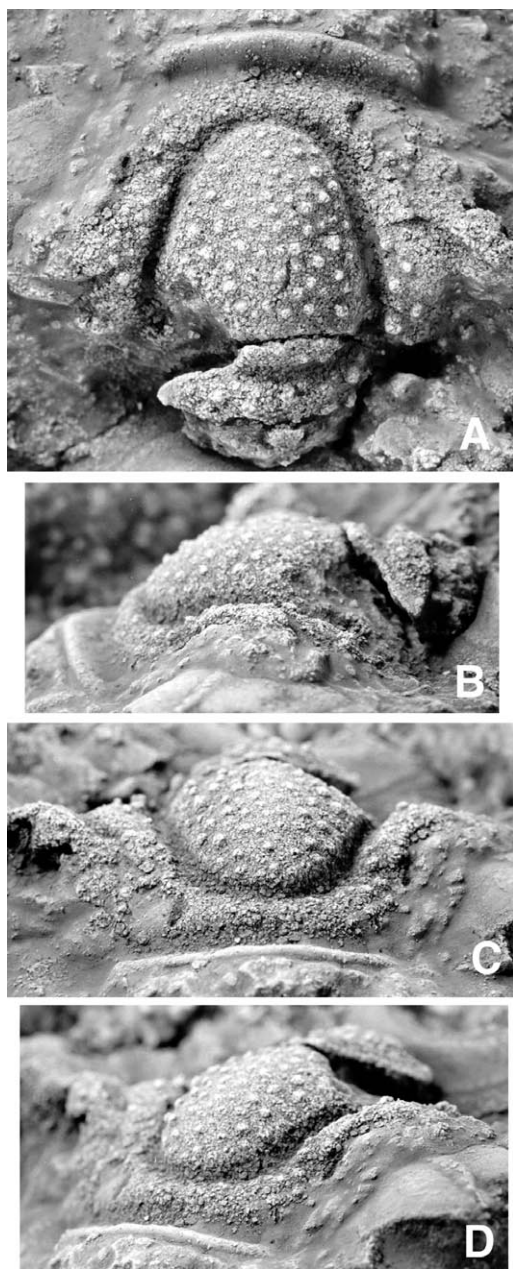


FIG. 3. *Hystricurus conicus* (Billings, 1859), holotype, GSC 516, from the Ogdensburg Member, Beauharnois Formation, Montreal area, Quebec, dorsal, left lateral, anterior and oblique views, $\times 3$.

MATERIAL AND OCCURRENCE. SUI 999736, 99737, Stairsian ('Zone F - *Rossaspis superciliosa* Zone'),

Fillmore Formation, Section G 48.5m, southern Confusion Range, Ibex area, Millard County, western Utah.

REMARKS. *Hystricurus oculilunatus* has been considered by Boyce (1989: 38-39) to be very widely distributed in North America. Almost all of these claims need to be investigated on the basis of much more abundant, better preserved, and better illustrated material than is presently available. Boyce's material from the Boat Harbour Formation of western Newfoundland appears to differ from *H. oculilunatus* in its much coarser tuberculate sculpture and much more laterally bowed palpebral furrow. *Hystricurus oculilunatus* differs from *Hystricurus* spp. nov. A and B in its narrow and more transversely arcuate frontal area, slightly less waisted glabella, and much more strongly tuberculate and spinose pygidium. It differs from *H. deflectus* in its anteriorly broader cranidium, longer palpebral lobes, and pygidia with less robust spines and a shorter vertical 'wall' beneath the pleurae.

***Hystricurus* sp. nov. A**
(Fig. 4B,F,J)

MATERIAL AND OCCURRENCE. SUI 99738 (Section FB7 102.1m), 99739 (Section HC5 106.7), Stairsian ('Zone E - *Tesselacauda* Zone'), Garden City Formation, Bear River Range, Franklin County, southeastern Idaho.

REMARKS. *Hystricurus* sp. nov. A is most similar to the stratigraphically younger species *Hystricurus* sp. nov. B., from which it differs in its shorter anterior border and pygidium with pleural spines prominently developed on, versus absent from, the second and third segments.

***Hystricurus* sp. nov. B**
(Fig. 4C,G,K)

MATERIAL AND OCCURRENCE. Assigned specimens SUI 99740, 99741, Stairsian (strata between Zones 'E' and 'F'), Fillmore Formation, Section G 26.6m, southern Confusion Range, Ibex area, Millard County, western Utah.

REMARKS. *Hystricurus* sp. nov. B was compared with *Hystricurus* sp. nov. A, which it closely resembles, above.

***Hystricurus* cf. *deflectus* Heller, 1956**
(Fig. 4D,H,L)

Hystricurus deflectus Heller, 1956: 43, pl. 18, fig. 6.

Hystricurus deflectus Heller; Boyce, 1989: 40, pl. 12, figs 1-10, pl. 13, figs 1-10 (with full synonymy).

MATERIAL AND OCCURRENCE. SUI 99742, 99743, Stairsian ('Zone D - *Leioptegium-Kainella* Zone'), Fillmore Formation, Section MME 22.3m.

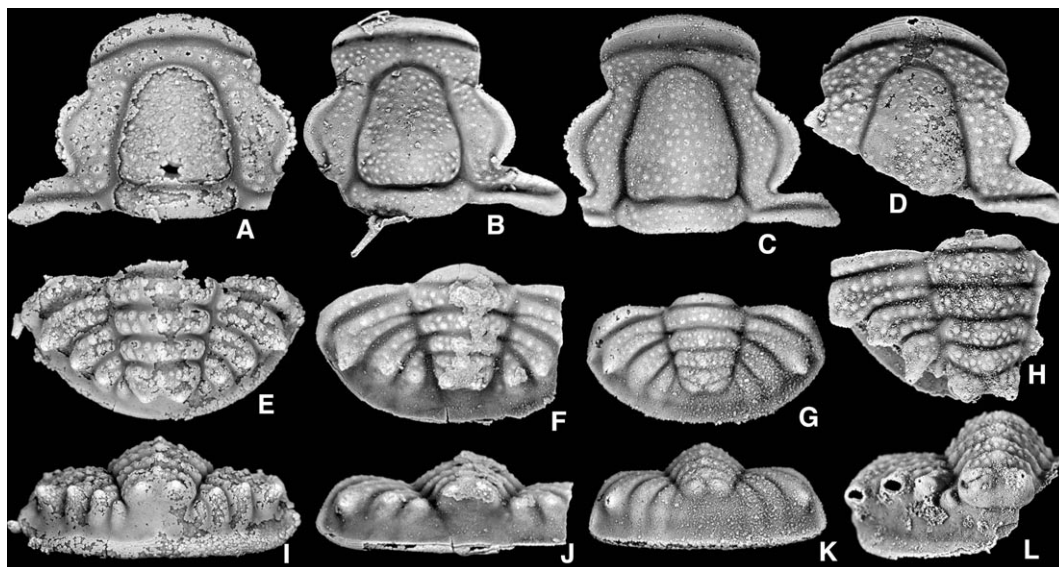


FIG. 4. *Hystricurus* spp. A, E, I, *Hystricurus oculilunatus* (Ross, 1951), Stairsian, Fillmore Formation, Section G 48.5m. A, cranidium, SUI 99736, dorsal view, $\times 5$. E, I, pygidium, SUI 99737, dorsal and posterior views, $\times 3.5$. B, F, J, *Hystricurus* sp. nov. A, Stairsian (Tesselacauda Zone), Garden City Formation. B, cranidium, SUI 99738, dorsal view, $\times 3.5$ (FB7 102.1m). F, J, pygidium, SUI 99739, dorsal and posterior views, $\times 6$ (HC5 106.7m). C, G, K, *Hystricurus* sp. nov. B, Stairsian, Fillmore Formation, Section G 26.6m. C, cranidium, SUI 99740, dorsal view, $\times 6$. G, K, pygidium, SUI 99741, dorsal and posterior views, $\times 6$. D, H, L, *Hystricurus* cf. *deflectus* Heller, 1956, Stairsian (Leiostegium-Kainella Zone), Fillmore Formation, Section MME 22.3m. D, cranidium, SUI 99742, dorsal view, $\times 5$. H, L, pygidium, SUI 99743, dorsal and posterior views, $\times 3.5$.

REMARKS. *Hystricurus deflectus* is not well known on the basis of Heller (1956). Boyce (1989) assigned material from the Boat Harbour Formation of western Newfoundland to Heller's species. Material from the lower Stairsian of the Fillmore Formation is closely comparable with Boyce's taxon, though probably not conspecific. The species are very similar in cranidial dimensions, particularly the narrow anterior part of the glabella. Pygidia are also most closely comparable, but the pleural furrows of Boyce's species run obliquely posterolaterally, whereas those of the Fillmore species are nearly transverse. The Fillmore species also has a broader pleural area proximal to the fulcrum and apparently even more pronounced pygidial spines.

Flectihystricurus gen. nov.

TYPE SPECIES. *Hystricurus flectimembrus* Ross, 1951, from the Stairsian of the Garden City Formation, southeastern Idaho.

OTHER SPECIES. *Hystricurus acumennasus* Ross, 1951, Stairsian, Garden City Formation, Idaho; *Hystricurus wilsoni* Gobbett, 1960, Stairsian, Lower Oslobreen Limestone, Spitsbergen.

DIAGNOSIS. Posterior fixigena nearly transversely straight and extended laterally; short median occipital spine flanked by at least one pair of shorter spines on occipital ring; cranial posterior border with short, posterodorsally directed spines; librigenal lateral border dorsoventrally flattened and lacking tuberculate sculpture; base of genal spine interrupting posterior/lateral border furrows and extending toward librigenal field; genal spine flattened and blade-like in section; pygidium with axis merged posteriorly with border, 4-5 axial rings.

REMARKS. *Flectihystricurus* comprises an easily recognised clade currently with 3 named species. Species of *Flectihystricurus* differ from those of *Hystricurus* in their relatively wider frontal areas, smaller eyes, spinose occipital ring and posterior cranial border, more elongate librigenae with blade-like genal spines, and pygidia with flattened pleurae, lacking a pair of terminal axial tubercles or spines.

Although known from relatively coarsely preserved material, *F. wilsoni* compares closely with Ross's Garden City taxa (Gobbett, 1960).

The main difference lies in the assigned pygidia, which appear to lack pleural spines. Both *F. acumennasus* and *F. flectimembrus* have thoracic segments (not figured) with prominent dorsally produced spines near the fulcrum, and small spines are also present in this position on the first pygidial segment. *Flectihystricurus wilsoni* does show the long fulcral spine on an isolated thoracic segment (Gobbett, 1960, pl. 15, fig. 14).

***Flectihystricurus flectimembrus* (Ross, 1951)**
(Fig. 5)

Hystricurus flectimembrus Ross, 1951: 48, pl. 10, figs 25, 26, 29-33, pl. 11, figs 16-18, 20-33.

MATERIAL AND OCCURRENCE. Topotypes SUI 99744-99750 from Section HC6 127.5-131.3m. Stairian ('Zone F - *Rossaspis superciliosa* Zone'), Garden City Formation, west side of Hillyard Canyon, Bear River Range, Franklin County, southeastern Idaho.

DIAGNOSIS. Anterior cranial border only slightly longer sagittally than exsagittally; librigena with tubercles scattered over most of field; pygidium with five axial rings, prominent pleural spine near fulcrum of first posterior pleural band, smaller spines set much closer to axis on second and third bands.

DESCRIPTION. Cranium with sagittal length (excluding median occipital spine) 60% of maximum width across posterior fixigenae; width across midpoint of palpebral lobes 67% maximum width; glabella width about 75% sagittal length (excluding L0); anterior border short, about 60% sagittal length of L0, decreasing in length abaxially, posterior aspect flat in profile and inclined steeply toward anterior border furrow, dorsal and anterior aspect convex in profile; anterior border furrow uniformly very short, deep and sharply inscribed, with median break in course to describe very shallow inverted 'V' shape; preglabellar field relatively long, with faint median furrow in smaller specimens; anterior sections of facial suture short, anteriorly divergent and only slightly bowed laterally; preglabellar field and frontal area with sculpture of evenly scattered moderate tubercles; palpebral lobe large, laterally protruded; palpebral furrow deep, subsemicircular forming rim around lobe; palpebral lobe in horizontal plane in anterior view, with a single arcuate row of fine tubercles around rim; interocular fixigena about as wide as sagittal length of preglabellar field, tuberculate sculpture more sparse than on frontal area or posterior fixigena; glabella only slightly inflated, with evenly spaced sculpture of moderate

tubercles, denser than on any other part of cranium; S1 and S2 discernible in large specimens as distinct incised furrows adjacent to axial furrow, but very short; axial furrow slightly anteriorly divergent in front of shallow junction with S0, deeper and gently anteriorly convergent in front of S1, with relatively sharp break in course to run into gently anteriorly arcuate preglabellar furrow, yielding subrectangular glabella outline in plan view; S0 long, deeper laterally than medially; L0 slightly longer sagittally than exsagittally, with short median spine running from posterior margin, flanked by two shorter spines with bases more anteriorly set, several additional short spines and tubercles; posterior border furrow long and shallow; posterior fixigena very short, with single transverse tubercle row on large specimens; posterior border longer and nearly lobate distal to fulcrum, extended nearly directly laterally, with sculpture of fine tubercles and very short posteriorly directed spines.

Librigena with field about 2.5 times as long (exsag.) as wide beneath midlength of eye; eye low and long; eye socle of single very narrow band, separated from visual surface by very narrow furrow and from field by slightly deeper furrow; field with sculpture of scattered fine to moderate tubercles on adaxial three quarters of area, with area near posterior border furrow, base of genal spine, and along lateral border furrow smooth; lateral border furrow shallow but not wholly effaced, interrupted posteriorly by base of genal spine; lateral border flattened, slightly narrower anteriorly than posteriorly, with sculpture of very fine terrace lines on dorsal and ventrolateral aspects; posterior border very narrow, terminating against base of genal spine; genal spine as long as remainder of librigena including anterior projection, somewhat flattened, with faintly impressed furrow running down dorsal aspect, sculpture lateral to furrow and ventrally of very closely spaced fine terrace lines, spine with strong posterior curvature and tapering gently to sharp tip; doublure separated from border by sharp break in slope, nearly flat, reaching beneath adaxial area of field; panderian notch absent.

Rostral plate, hypostome and thorax not yet identified.

Pygidium with sagittal length 50% maximum anterior width; axis narrow, occupying 30% of anterior width; well-defined border around pygidium, broader laterally; margin broadly laterally convex posteriorly, with modest anterior

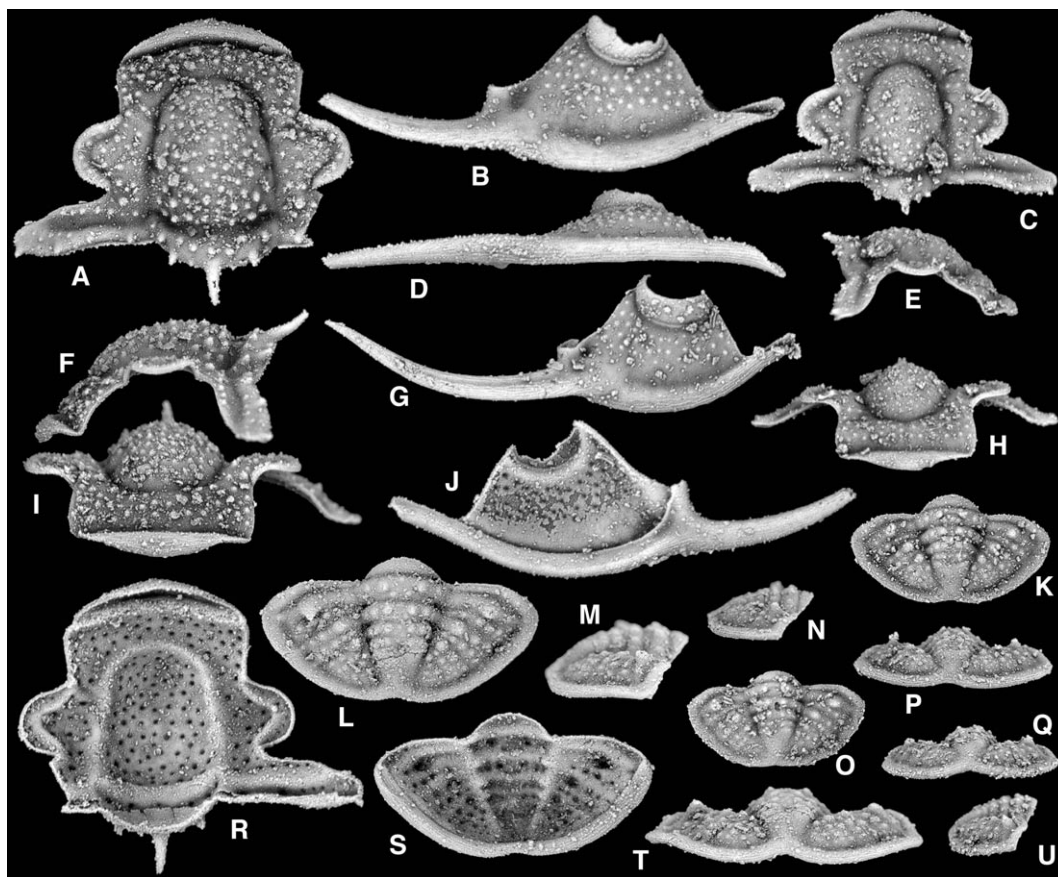


FIG. 5. *Flectihystricurus flectimembrus* (Ross, 1951), from the Garden City Formation (Stairsian, *Rossaspis superciliosa* Zone). A, F, I, R, cranidium, SUI 99744, dorsal, left lateral, anterior and ventral views, $\times 7.5$ (HC6 131.3m). B, D, J, right librigena, SUI 99745, external, ventrolateral and internal views, $\times 7.5$ (HC6 131.3m). C, E, H, cranidium, SUI 99746, dorsal, right lateral and anterior views, $\times 10$ (HC6 131.3m). G, right librigena, SUI 99747, external view, $\times 7.5$ (HC6 131.3m). K, N, P, pygidium, SUI 99748, dorsal, right lateral and posterior views, $\times 7.5$ (HC6, 127.5m). L, M, S, T, pygidium, SUI 99749, dorsal, right lateral, ventral and posterior views, $\times 7.5$ (HC6 127.5m). O, Q, U, pygidium, SUI 99750, dorsal, posterior and right lateral views, $\times 7.5$ (HC6 127.5m).

inflection medially, gently expressed as dorsal inflection in posterior view; axial rings 5, fifth very faintly defined, short, faint pseudo-articulating half ring on second segment only, with sculpture of pair of larger tubercles and scattered very fine tubercles, becoming minute posteriorly; axial furrows shallow and narrow, evenly convergent posteriorly; ring furrows with deep lateral 'slots,' but shallow medially, only first and second fully inscribed medially; elongate terminal piece grades into posteromedian pygidial border; pleural and interpleural furrows defined on first four segments, fourth very faint; posterior pleural band of first segment about

twice length of anterior band, bands of posterior segments more nearly subequal in length; first posterior pleural band with prominent short spine just distal to fulcrum; second and third segments with much smaller spines/tubercles set nearer to axis; anterior and posterior pleural bands of segments posterior to first with additional transverse row of fine tubercles; doublure narrow, wider laterally than medially, with sculpture of closely spaced fine terrace lines.

REMARKS. *Flectihystricurus flectimembrus* differs from *F. acumennasus* in the lack of that species' large, subtriangular anteromedian extension of the anterior border furrow, longer

preglabellar field, shorter subsidiary occipital spines, librigena with a greater number of tubercles occupying larger area of field, less effaced lateral border furrow, and less flattened lateral border and genal spine. It differs from *F. wilsoni* in its less inflated glabella, less dense cranial tuberculate sculpture, librigenal field with tuberculate sculpture effaced along lateral border furrow, versus much more densely and broadly distributed, more blade-like lateral border and genal spine, and pygidium with pleural spines present versus absent. In librigenal morphology, *F. flectimembrus* is intermediate between the more conventional morphology of *F. wilsoni*, in which the lateral border and genal spine are more nearly tubular and the field is densely tuberculate, and *F. acumennasus*, in which the tuberculate sculpture is restricted to an area beneath the eye, the lateral border furrow is partially effaced, and the lateral border and genal spine are most plainly blade-like.

Subfamily HINTZECURINAE subfam. nov.

INCLUDED GENERA. *Genalaticurus* gen. nov.; *Hintzecurus* gen. nov.; *Ibexicurus* gen. nov.; *Lavadamia* gen. nov.; *Politicurus* gen. nov.; *Rossicurus* gen. nov.

DIAGNOSIS. Hystricurid trilobites with relatively small pygidia usually with only 2-3 axial rings; anterior sections of facial sutures long, cranidia broad anteriorly and subquadrate excluding posterior fixigenae; librigenal field relatively small; thorax (as far as is known) of 9-10 segments with axial spine on sixth (axial spines, tentatively, appear to occur in all species based on association of disarticulated segments).

REMARKS. Hintzecurines share a suite of apomorphies distinguishing them from other hystricurids. Comparison is made below with Hystricurinae, because that is presently the only other putative hystricurid clade recognised. However, Hintzecurinae appears to be monophyletic in light of emerging knowledge of both the remainder of the hystricurids and potential Cambrian relatives such as the marjumioids.

Hintzecurines are plainly differentiated from the hystricurines in cranial and pygidial details. All known hystricurids have at least three fully and completely expressed pygidial segments, and often more. Hystricurine pygidia always bear prominent spines on the posterior pleural bands, while hintzecurines never do. Hystricurines have much larger eyes, resulting in much larger

palpebral lobes. In addition, their posterior fixigenae are typically extended transversely, while the anterior sections of the facial sutures are very short. As a result, hystricurine cranidia are much more anteriorly restricted than those of hintzecurines, but considerably broader posteriorly. The glabellae of hystricurines are typically fiddle-shaped, with a distinct anterior waisting, versus more or less evenly bullet-shaped in hintzecurines. Hystricurine librigenae, in addition to features associated with the much larger eyes, typically have a larger and relatively much longer field, and are less flexed in ventrolateral view.

Hintzecurines appear to be restricted in occurrence to the upper Skullrockian. In the most completely fossiliferous and best sampled section, they appear at the very top of the Barn Canyon Member in strata assigned by Loch et al. (1999) to the *Symphysurina bulbosa* Subzone). When sampling resumes at the base of the Red Canyon Member, hintzecurines are abundant, with two or three species tentatively assigned to *Ibexicurus* at every sample horizon from LDN 77m through LDN 111m. Additional genera (some undescribed) then make their first appearance. *Politicurus*, *Hintzecurus*, and *Rossicurus* all appear at horizon LDN 128.2. This also marks the last appearance of *Ibexicurus*, and the only known horizon at which *Ibexicurus* occurs with the former genera. The 'Bellefontina-Xenostegium Zone' can therefore be subdivided into a lower *Ibexicurus* Interval and an upper *Politicurus* Interval (Fig. 2).

Hintzecurus gen. nov.

TYPE SPECIES. *Hystricurus paragenalatus* Ross, 1951, from the Garden City Formation, Ibexian (Skullrockian), Idaho.

OTHER SPECIES. At least two undescribed new species in the Red Canyon Member, House Formation, Ibex area, Utah: *Hintzecurus* sp. nov. 1, LDN 128.2-132.0m and EEE 95.0m; *Hintzecurus* sp. nov. 2, LDN 146.5m.

ETYMOLOGY. After Lehi F. Hintze, in recognition of his superb pioneering work on the trilobite faunas of the Pogonip Group in the Ibex region.

DIAGNOSIS. Cranidium broad, with posteriorly directed spines along some or all of posterior margin of posterior border; genal field small, narrow with only a few tubercles; genal spine slender, tuberculate, strongly curved; pygidia with broad posterolateral pleurae and only weak posteromedian embayment.

REMARKS. *Hintzecurus* is ubiquitous from horizon LDN 128.2m through LDN 148.7m in the Red Canyon Member, House Formation, represented by *H. paragenalatus* and two new, undescribed species in our collections.

***Hintzecurus paragenalatus* (Ross, 1951)**
(Fig. 6)

Hystricurus paragenalatus Ross, 1951: 42, pl. 8, figs 14-26.
Indefinitely assigned pygidia from zone 'B'; Ross, 1951: pl. 9, figs 3,4,6,8,9,11,17 [only].

MATERIAL AND OCCURRENCE. Topotypes SUI 99569-99574 from Section FB7 39.0-44.2m, Garden City Formation, Franklin Basin, Bear River Range, Franklin County, southeastern Idaho. SUI 99751 from Section LDN 144.0m, Red Canyon Member, House Formation, southern House Range, Ibex area, Millard County, western Utah. All Skullrockian ('Zone B - *Bellefontia-Xenostegium* Zone').

DIAGNOSIS. Glabella relatively small; anterior border relatively long, dorsally smooth; posterior cranial border with fringe of short posteriorly directed spines extended along most of width; genal spine very long, curved, with posterolateral fringe of small spines; pygidium with tuberculate sculpture on anterior axial rings and pleural bands.

DESCRIPTION. Cranidium (excluding posterior fixigenae) subquadrate, with length slightly less than 90% of width across palpebral lobes; width across palpebral lobes about 75 % of width across posterior fixigenae; glabella gently tapered and well-rounded anteriorly, occupying about 70% of cranial length and slightly more than 40% of cranial width across palpebral lobes; strongly convex, raised well above fixigenae and accounting for about 60% of cranial height in anterior view; longitudinal profile of glabella curved gently upward from occipital furrow to reach maximum height opposite palpebral lobes, then curved gradually downward to preglabellar furrow; axial and preglabellar furrows firmly impressed grooves; occipital furrow well-incised, nearly transverse medially but curved strongly forward towards axial furrow; occipital ring accounts for about 20 % of glabellar length; S1 and S2 expressed near axial furrow as narrow, oblique bands that lack sculpture; L1 about 120% length of occipital ring; L2 equal to length of occipital ring; frontal lobe occupies about 33% of glabellar length; frontal area divided into convex, forwardly curved border and downsloping preglabellar field by well-defined border furrow; border slightly less than 50 % of frontal area length; arcuate palpebral lobe nearly flat, raised slightly

above fixigena, centred opposite S1 furrow; length about 33% of glabellar length; palpebral furrow well-incised, arcuate groove; palpebral ridge absent; interocular fixigena broad, equal to slightly less than 50% of glabellar width across S1 furrows, and sloping steeply upward from axial furrow to become nearly flat adjacent to palpebral furrow; anterior sections of facial sutures initially divergent, before swinging inward at, or just behind, anterior border furrow; posterior sections strongly divergent before curving backward at posterior border furrow, so that course is weakly sigmoidal; posterior fixigenae with firmly impressed posterior border furrow; border convex and equal to slightly less than 10% of glabellar length; glabella, fixigenae and anterior half of anterior border with sculpture of small, closely-spaced tubercles; row of prominent, spine-like tubercles present along posterior margin of L0; similar tubercles form row along posterior margin of posterior border, decreasing in size laterally away from glabella, with larger tubercle at posterior corner of cranidium.

Librigena with long, curved genal spine equal to about 300% length of librigenal field; field broad, subtrapezoidal in outline, and steeply upsloping; visual surface of eye mounted on narrow, wire-like eye socle; lateral border furrow expressed only below anterior 1/2 to 2/3 of librigenal field; lateral border convex anteriorly, merging with librigenal field posteriorly; posterior border furrow well-defined; convex posterior border extending onto genal spine as weak, carinate ridge; convex doublure extending inward as far as lateral and posterior borders; upper half of librigenal field with small, closely-spaced tubercles; lateral border with coarse granules; outer edge of genal spine with row of coarse tubercles; posterior border with row of small, spine-like tubercles, similar to those along posterior margin of cranidium, that extend for short distance along inner edge of genal spine; doublure with fine terrace ridges.

Rostral plate not recovered. Hypostome not identified.

Thorax of 9 segments, with axial spine on the sixth; segment 1 same width as segment 5, segment 2 same width as segment 4; segment 3 widest in thorax; segments posterior to 3 narrow gradually and evenly so that thoracic lateral margin and pygidial margin describe even curve; pleural tips of segments 1-6 with single short posteriorly-directed spine, tips of segments 7-9 subquadrate and lacking spines; axial rings of

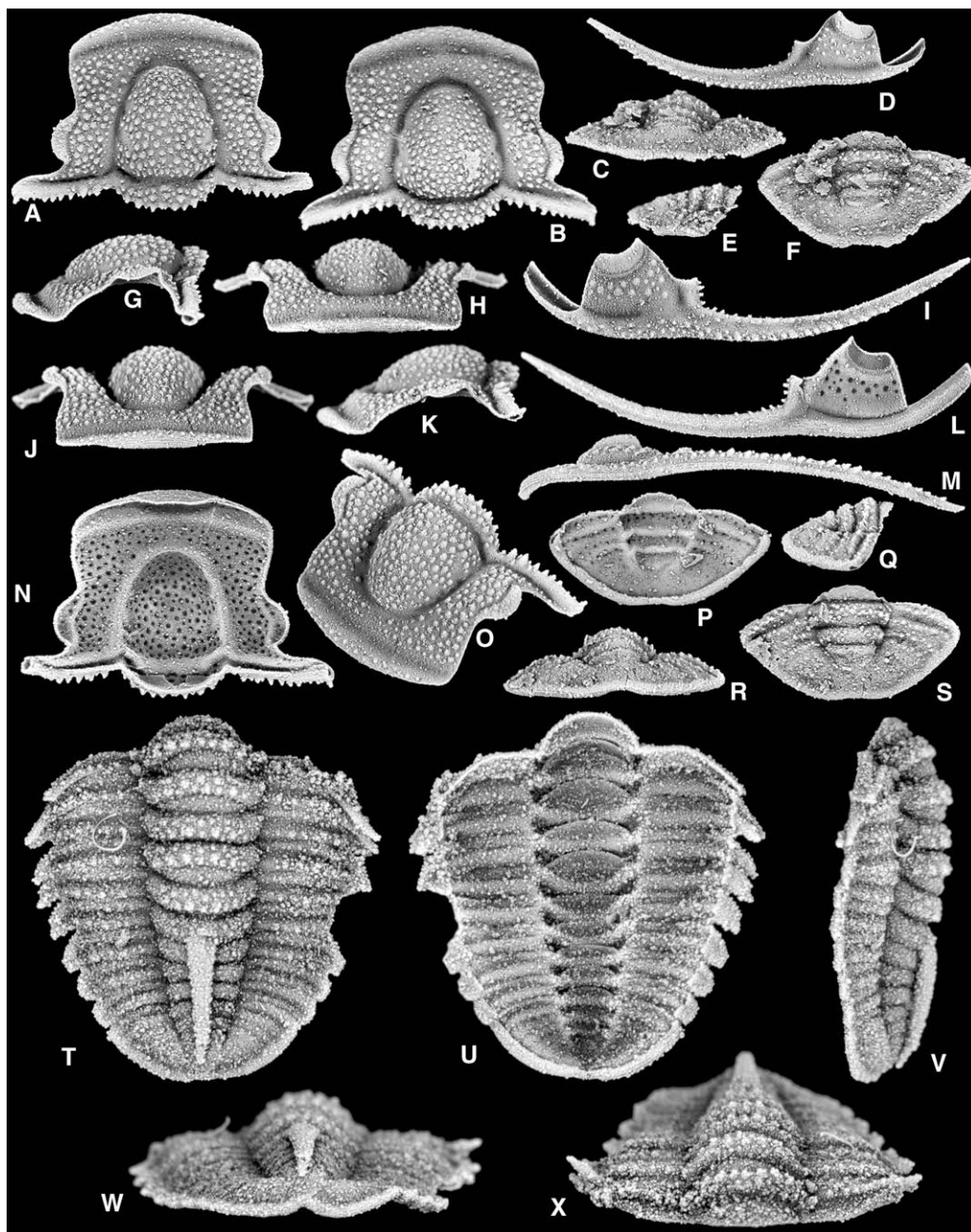


FIG. 6. *Hintzecurus paragenalatus* (Ross, 1951). A-S from the Garden City Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Franklin Basin, section FB7 39.0-44.2m; topotype material. A, G, J, N, O, cranidium, SUI 99569, dorsal, left lateral, anterior, ventral and oblique views, $\times 6$. B, H, K, cranidium, SUI 99570, dorsal, anterior and left lateral views, $\times 6$. C, E, F, pygidium, SUI 99571, posterior, right lateral and dorsal views, $\times 7.5$. D, right librigena, SUI 99572, external view, $\times 6$. I, L, M, left librigena, SUI 99573, external, internal and ventrolateral views, $\times 6$. P-S, pygidium, SUI 99574, ventral, right lateral, posterior and dorsal views, $\times 7.5$. T-X from the Red Canyon Member, House Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Ibex area, section Lava Dam North 144.0m, thoracopygidium, SUI 99751, dorsal, ventral, left lateral, posterior and anterior views, $\times 7.5$.

segments 1-5 with strong and dense tuberculate sculpture, ring of segment 6 with weaker tubercles around thick median spine based, rings of segments 7-9 lacking tuberculate sculpture; anterior and posterior pleural bands of all segments subequal in length; pleural furrow long, shallow, and nearly straight; fulcrum very distally set, most of pleural lobe proximal to fulcrum; pleurae of segments 1-7 with transverse tubercle rows on pleural bands, much stronger on posterior bands; pleural bands of segments 8 and 9 with only very fine and widely scattered tubercles; axial furrow deep, narrow on all segments; axial spine on sixth segment thick at base but tapering rapidly distally, not extending to posterior border of pygidium, posteriorly directed and apparently held subparallel to and immediately on top of posterior thoracic and pygidial axial rings; pleural tips of all segments except 1 and 2 underlain by broad (tr.) doublure with anteroposteriorly directed short terrace lines.

Pygidium subtrapezoidal, with nearly transverse posterior margin; maximum width slightly less than twice length; weakly convex, with maximum height in posterior view about 30% of maximum width; axis moderately convex, accounting for about half of pygidial height in posterior view, short, occupying slightly less than 70% of pygidial length, and gently tapered, maximum width equal to about 33% of maximum cranial width; axial furrows shallow grooves; three axial rings and terminal piece decrease progressively in length posteriorly, so that terminal piece equal to about 80% of length of anteriormost ring; ring furrows well incised, nearly transverse; semielliptical articulating half ring equal to about half length of anteriormost axial ring; pleural fields very weakly inflated near axial furrow, then slope gently downward towards border; anteriormost pleural furrow well-incised, upto 2 additional faint furrows may be evident on pleural field; interpleural furrows barely perceptible; gently convex border separated from pleural field by shallow border furrow; arched weakly upward behind axis in posterior view; axial rings and pleural bands with fine granules; pygidial doublure with fine terrace ridges.

REMARKS. Two obviously distinct undescribed species of the genus have been identified from the Red Canyon Member, House Formation. *Hintzecurus paragenalatus* differs from an older species from LDN 128.2-132m and EEE 95m

particularly in the much longer and much more curved genal spines. It differs from a younger species from LDN 146.5m most strikingly in the dense, small, posteriorly directed spines over most of the posterior aspect of the cranial posterior border, versus restricted to the adaxial part in the younger species, and in the pygidium with a distinct tuberculate sculpture on the axial rings and at least anterior pleural areas, versus almost entirely smooth in the younger species.

***Ibexicurus* gen. nov.**

TYPE SPECIES. *Ibexicurus parsonsi* from the House Formation, Ibexian (Skullrockian), Utah.

OTHER SPECIES. *Hystricurus hillyardensis* Stitt, 1983; ?*Hystricurus ravni* Poulsen, 1927; more than a dozen undescribed hintzecurine species occur in the *Ibexicurus* Interval of the Red Canyon Member at Ibex, some or all of which are assignable to *Ibexicurus* (see Remarks below).

ETYMOLOGY. For the Ibex area.

DIAGNOSIS. Preglabellar field long; cranidium relatively vaulted; palpebral furrows weakly inscribed; pygidium relatively large, with broad pleurae with subdued or absent tuberculate sculpture.

REMARKS. There are many undescribed hintzecurine species from the lower *Ibexicurus* Interval of the Red Canyon Member, and most of them will probably be referable to *Ibexicurus*. Precise hypotheses of the phylogenetic structure of the subfamily must await full description of all its members and cladistic analysis, but care has been taken to select a type species for *Ibexicurus* that is representative of a distinct, apparently monophyletic, subset of the species occurring in the *Ibexicurus* interval. Other of the *Ibexicurus* Interval species are apparently plesiomorphic.

Hystricurus hillyardensis was erected by Stitt (1983) from the McKenzie Hill Limestone of Oklahoma. The name, however, was in reference to *Hystricurus* sp. D of Ross (1951), which Stitt considered conspecific with the Oklahoma specimens and which occurs at Hillyard Canyon. Stitt also considered '*Hystricurus* cf. *H.* sp. D Ross' of Winston & Nicholls (1967), from the Wilberns Formation of central Texas conspecific with his new taxon and considered (1983, p. 25) *H. hillyardensis* 'a widespread and stratigraphically useful taxon'. In our opinion, the association of sclerites in the illustrated Oklahoma material is incorrect, and the 3 occurrences are collectively so poorly documented that it is barely possible to assess their relationships, let

alone support a claim of conspecificity. The Oklahoma specimens, however, are almost certainly not conspecific with the Garden City material. Ross's (1951) '*Hystericurus* sp. D' was based on 2 incomplete crackout cranidia from HC5. They have a broad, inflated, quite coarsely tuberculate, glabella and a short (sag., exsag.), broad anterior border with a narrowly incised border furrow. The holotype cranidium of *H. hillyardensis*, in contrast, has a narrow, less robustly tuberculate, glabella and a long anterior border, with a shallow border furrow that is uneven in depth along its course. A second cranidium assigned by Stitt (1983, pl. 4, fig. 4) from a separate section and horizon is more similar, but is doubtfully conspecific with the holotype. The three cranidia figured by Winston & Nicholls (1967) are so incomplete and poorly illustrated as to be uninterpretable.

There are several undescribed species in the lower *Ibexicurus* Interval of the Red Canyon Member of the House Formation which are clearly related to *I. hillyardensis* and show that the holotype cranidium and paratype librigena illustrated by Stitt (1983, pl. 4, figs 3, 5) are definitely correctly associated, but that the pygidium is likely not. It is unfortunate that *I. hillyardensis* was erected on the basis of such sparse and incompletely known material.

***Ibexicurus parsonsi* sp. nov.**
(Fig. 7)

ETYMOLOGY. For Gram Parsons.

MATERIAL AND OCCURRENCE. Holotype SUI 99599 and paratypes SUI 99600-99602 from Section LDN 115.6m, Skullrockian ('Zone B - Bellefontia-Xenostegium Zone'), Red Canyon Member, House Formation, southern House Range, Ibex area, Millard County, western Utah. Known only from type horizon.

DIAGNOSIS. Interocular fixigenae broad; cranidium with relatively widely spaced sculpture of moderate sized tubercles, more dense on glabella; librigenal field only sparsely tuberculate; pygidium broad and with dorsal sculpture considerably effaced.

DESCRIPTION. Cranidium with sagittal length about 65% maximum width across posterior fixigenae; width across midpoint of palpebral lobes about 77% width across posterior fixigenae; glabella occupying about 70% of cranial sagittal length; maximum width of glabella achieved across rear of L1, slightly less than sagittal length excluding L0; anterior border

with strong dorsal convexity in sagittal profile, tubular, but with flatter anteromarginal aspect; moderate tubercles on anterodorsal and anterior aspect, none along posterior part; anterior border furrow deep, short (sag., exsag.), and incised, course not evenly arcuate but very slightly deflected posteriorly in two places on either side of midline; anterior border furrow, slight deflections excepted, and anterior border describing a convex forward very shallow transverse arc, more transversely straight medially; anterior sections of facial suture strongly bowed laterally, reaching maximum divergence opposite rear part of preglabellar field, maximum point of divergence in front of adaxial one third of palpebral lobes; preglabellar field quite long, about 18% of sagittal length of cranidium in plan view, with moderate dorsal inflation independent of slope of anterior part of glabella in sagittal profile; broad frontal area and preglabellar field with sculpture of fairly large, uniform, widely spaced, prominent tubercles; interocular fixigena broad and dorsally convex, with tuberculate sculpture similar to that on frontal area, except tubercles slightly smaller and more densely crowded, absent from smooth strip adjacent to axial furrow; palpebral furrow shallow but more or less distinct, bowed slightly laterally opposite main body of palpebral lobe; palpebral lobe moderately large, protruded laterally, in horizontal plane in anterior profile, with sculpture of 4-5 small tubercles in row parallel with lateral margin; axial furrow shallow posteriorly, junction of axial, occipital, and posterior border furrows forms smooth subtriangular depressions opposite rear of glabella; axial furrows gently anteriorly convergent in front of this depression, bow in to form subtle constriction of glabella just in front of anterior edge of palpebral lobes, strongly anteriorly convergent in front of this and running smoothly into preglabellar furrow; preglabellar and anterior part of axial furrow of similar depth, deeper than posterior part of axial furrow; glabella subquadrate to bullet-shaped, only moderately inflated in sagittal profile, though distinctly elevated above remainder of cranidium in anterior profile, with sculpture of tubercles of similar size to those on interocular fixigenae, but much more densely crowded - glabellar tuberculate sculpture is densest of entire cephalon; glabellar furrows not incised, reflected as very slight lateral depressions and smooth areas adjacent to axial furrow; S0 deep abaxially, immediately adjacent to smooth triangular area marking junction with posterior border furrow

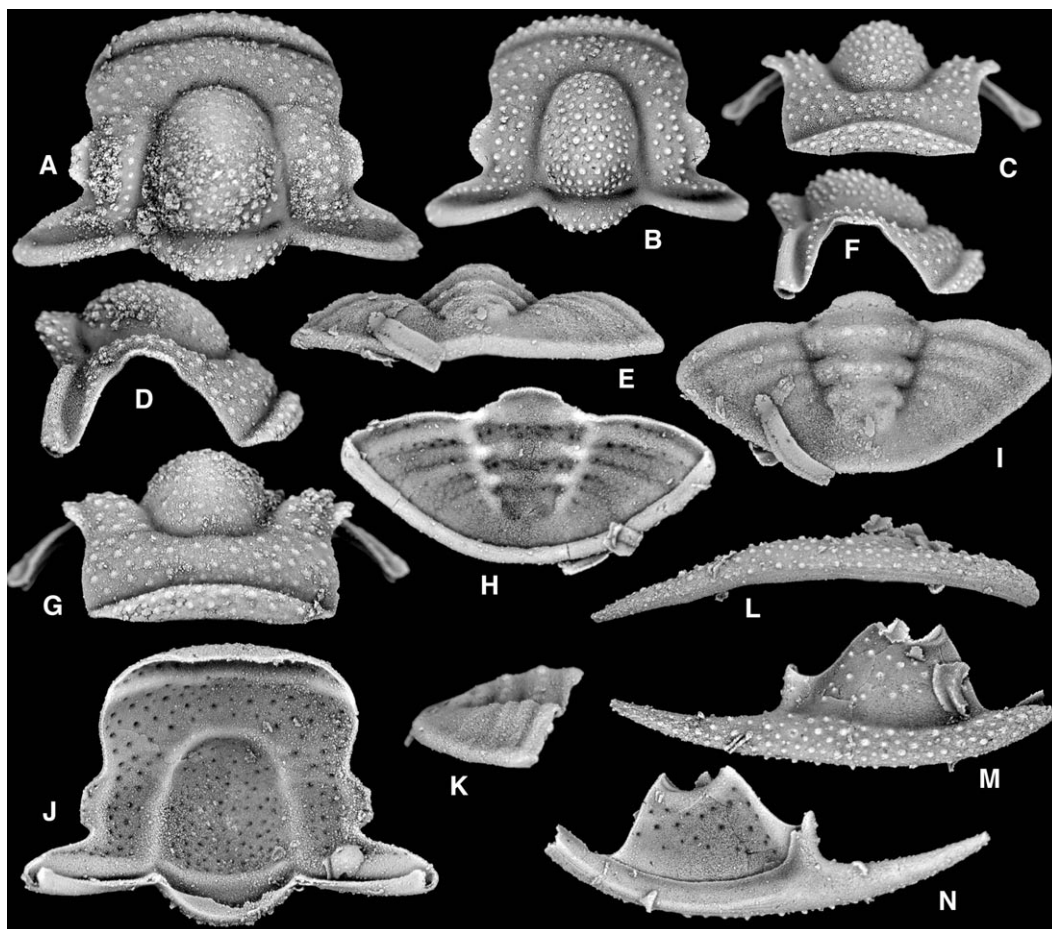


FIG. 7. *Ibexicurus parsonsi* gen. et sp. nov., from the Red Canyon Member, House Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Ibex area, section Lava Dam North 115.6m. A, D, G, J, cranium, holotype, SUI 99599, dorsal, right lateral, anterior and ventral views, $\times 5$. B, C, F, cranium, SUI 99600, dorsal, anterior and right lateral views, $\times 6$. E, H, I, K, pygidium, SUI 99601, posterior, ventral, dorsal and right lateral views, $\times 6$. L-N, right librigena, SUI 99602, ventrolateral, external and internal views, $\times 6$.

and axial furrows, shallower medially; L0 long, longer sagittally than exsagittally, with sculpture of mixed moderate and fine tubercles mainly on posterior part; anterior part sloping into shallowed median part of S0 smooth; posterior border furrow long, relatively shallow, shortest (exsag.) and deepest on proximal part; posterior border lengthening steadily abaxially, devoid of sculpture except for a few very fine tubercles on posterior edge proximally.

Librigena with width at midpoint of eye slightly less than half maximum exsagittal length; genal spine about 80% exsagittal length of remainder of librigena excluding anterior

projection; posterior border furrow and posterior part of lateral border furrow shallow, meeting at acute posterior 'point' above base of genal spine; lateral border furrow becoming deeper anteriorly; field with relatively sparse sculpture of fine to moderate sized tubercles, entirely smooth in area adjacent to lateral border furrow; eye socle of single band, more prominent in thicker anterior lobe; lateral border convex and densely tuberculate, with finer tubercles arranged in rows along ventrolateral aspect; lateral border wider posteriorly, narrowing opposite midpoint of eye; genal spine with tuberculate sculpture similar to that of posterior part of lateral

border, stout at base, tapering evenly and rapidly posterior to moderately blunt tip, with slight posterior curvature; doublure sharply inturned from ventrolateral edge of lateral border, creating distinct ridge along inturn, extended medially completely across ventral aspect of lateral border furrow, forming shallow angle under base of genal spine, panderian notch absent.

Rostral plate unknown. Hypostome not identified. Thorax not yet identified, but abundant isolated segments bearing axial spines occur at the type horizon, some of which almost certainly belong to the species.

Pygidium with sagittal length (including articulating half ring) slightly less than half maximum width; axis quite narrow, occupying just less than a third of pygidial width at broadest point anteriorly; axis with maximum width about 85% sagittal length; pygidium with subdued dorsal sculpture, large but partly effaced tubercles on first and second axial rings, very faint tubercles on third; tubercles on adaxial half of anterior and posterior pleural bands of first segment, only on very adaxial part of bands of second segment, and indiscernible on pleurae of third segment; axis with three defined axial rings and effaced terminal piece; axial furrows shallow, evenly convergent posteriorly, axis weakly but fully defined posteriorly, with posterior extent well in front of median part of pygidial border; ring furrows much deeper abaxially near contact with axial furrow, slot-like, but shallow medially; 3 ring furrows developed, though third is quite subtle; nearly effaced pseudo-articulating half ring on second segment; first pleural furrow shallow but distinct to contact with inner edge of border; posterior interpleural and pleural furrows increasingly shallower and effaced; anterior and posterior pleural bands subequal in length (exsag.); border distinct anteriorly, quite broad, less distinct from effaced pleurae posteriorly, clearest in posterior profile; doublure slightly broader laterally, narrowest medially.

REMARKS. *Ibexicurus parsonsi* is distinguished from most of the many undescribed species of the genus in the Red Canyon Member of the House Formation by its relatively broad interocular fixigena, sparsely tuberculate librigenal field, relatively short genal spine, and broad, considerably effaced pygidium.

Rossicurus gen. nov.

TYPE SPECIES. *Hystricurus lepidus* Hintze, 1953, from the House Formation, Ibexian (Skullrockian), Utah.

OTHER SPECIES. *Rossicurus* sp. nov. 1 (LDN 128.2-132.0); *Rossicurus* sp. nov. 2 (LDN 135.5m); *Rossicurus* sp. nov. 3 (LDN 142.0-144.2m), *Rossicurus* sp. nov. 4 (HC5 38.1m).

ETYMOLOGY. After Rueben J. Ross, Jr., in recognition of his superb pioneering work on the trilobite faunas of the Garden City Formation in southern Idaho and northern Utah.

DIAGNOSIS. Hintzecurines with very vaulted cephalae, broad librigenal fields, short to very short genal spines, and small, narrow pygidia which are either smooth or which bear a characteristic single knob-like tubercle on the adaxial part of the posterior pleural band of the first segment.

REMARKS. Hintze (1953) established the type species on the basis of 3 sclerites, the holotype cranidium and two librigenae, from his locality E-13 in Section E, Middle Mountain, regarded as 'high Zone B'. It is now apparent that Hintze's holotype is not conspecific with the assigned librigenae, which clearly belong to *Politicurus*. In collections at Middle Mountain (our Section MME) and the House Range (LDN), *Rossicurus lepidus* is restricted to the very highest (approx. 2m) interval of the 'Bellefontia-Xenostegium Zone' and is part of the last diverse Red Canyon Member fauna. It cooccurs with undescribed new species of *Politicurus* (to which Hintze's [1953] paratype librigenae belong), *Hintzecurus* and *Genalaticurus*. *Rossicurus* appears at the same time as *Politicurus* and *Hintzecurus* at the base of the *Politicurus* Interval, and is ubiquitous and often common at all horizons through the interval.

Rossicurus lepidus (Hintze, 1953) (Fig. 8)

Hystricurus lepidus Hintze, 1953: 166, pl. 7, figs 12a-c [not figs 10a,b, 11, =*Politicurus* sp. nov.].

MATERIAL AND OCCURRENCE. SUI 99575-99580, from Section LDN 146.5m, Skullrockian ('Zone B - Bellefontia-Xenostegium Zone'), Red Canyon Member, House Formation, southern House Range, Ibex area, Millard County, western Utah. Hintze's (1953). Holotype is from his sampling horizon E-13, at 385' (117.3m) in his Section E, Middle Mountain, Ibex area, Utah.

DIAGNOSIS. Posterior fixigena with very little lateral protrusion; anterior border very strongly transversely arched in anterior view; cephalon strongly vaulted; librigenal field broad; genal spine short; pygidium small and narrow, with prominent border and lacking tuberculate sculpture except for large knob-like tubercles on ad-

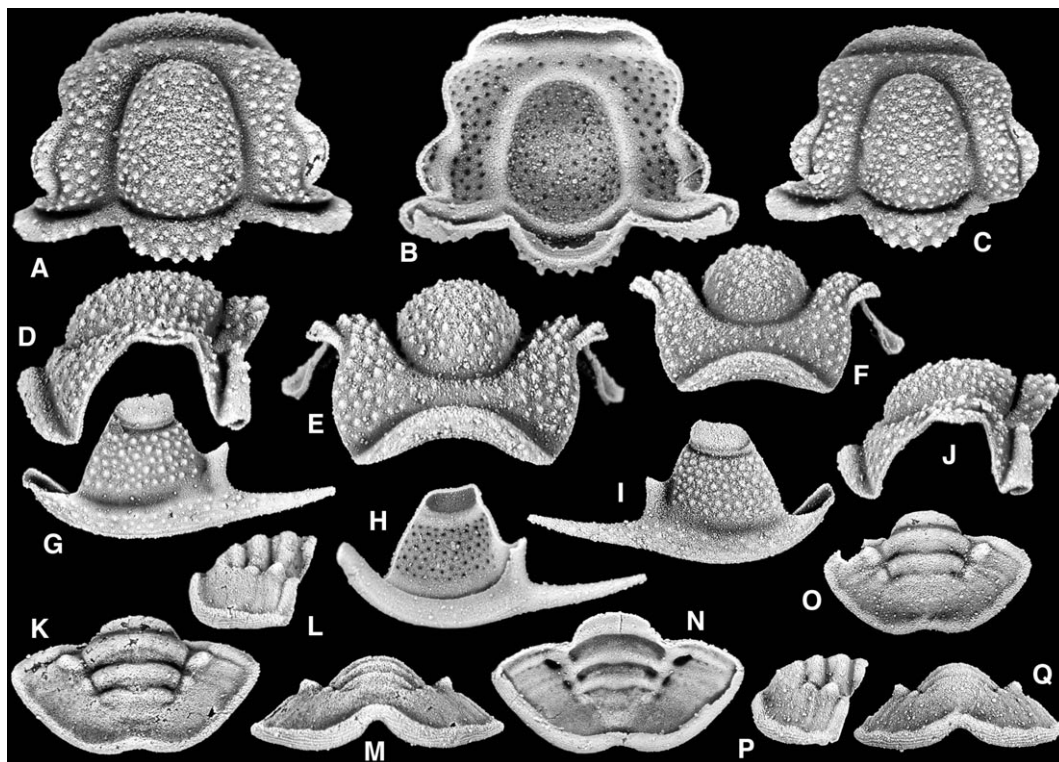


FIG. 8. *Rossicurus lepidus* (Hintze, 1953), from the Red Canyon Member, House Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Ibex area, section Lava Dam North 146.5m. A, B, D, E, cranidium, SUI 99575, dorsal, ventral, left lateral and anterior views, $\times 10$. C, F, J, cranidium, SUI 99576, dorsal, anterior and left lateral views, $\times 10$. G, left librigena, SUI 99577, external view, $\times 7.5$. H, I, right librigena, SUI 99578, internal and external views, $\times 7.5$. K-N, pygidium, SUI 99579, dorsal, right lateral, posterior and ventral views, $\times 7.5$. O-Q, pygidium, SUI 99580, right lateral, dorsal and posterior views, $\times 7.5$.

axial part of posterior pleural band of first segment and smaller repetition on second segment.

DESCRIPTION. Cranidium with sagittal length about 70% of maximum width across posterior fixigenae; width across midpoint of palpebral lobes about 90% of maximum width; glabella occupying 80% of sagittal cranidial length in plan view; glabella with maximum width opposite midpoint of palpebral lobes, occupying 40% cranidial width across palpebral lobes; glabellar maximum width 80% length excluding L0; anterior border with moderate dorsal and anterior convexity, not as 'tubular' as in many other hintzeurines, lacking sculpture dorsally, sculpture of subdued tubercles and terrace lines on anterior aspect; anterior border relatively short (sag., exsag.), longest medially, tapering in length laterally; anterior margin not transverse but broadly arcuate; anterior border strongly

transversely bowed in anterior view; anterior border furrow running nearly transversely, with only slight anterior arch, moderately deep, short (sag., exsag.) and incised; preglabellar field short, about same sagittal length as anterior border in plan view, with only minor independent dorsal inflation in sagittal profile; anterior sections of facial suture strongly bowed laterally, giving frontal area lobate appearance, maximum point of divergence set anteriorly just behind median part of anterior border furrow; interocular fixigena broad, narrowest opposite front of palpebral lobe; posterior fixigena forming very short (exsag.) strip in front of posterior border furrow; posterior fixigena, interocular fixigena, and frontal area with similar sculpture of nearly thorn-like moderate sized tubercles, sculpture more sparse and subdued on preglabellar field; palpebral furrow well incised

and distinct, bowed strongly laterally; palpebral lobe crescentic, nearly ridge-like, narrow, with sculpture of scattered fine tubercles; palpebral lobe about 1/3 length of cranium; axial furrow distinctly shallower than S0 or posterior border furrow, junction of three furrows forms shallow area on adaxial part of posterior fixigena; axial furrows initially slightly anteriorly divergent, then anteriorly convergent in front of rear of palpebral lobe, joining at slight angle (best seen ventrally) with anteriorly arcuate preglabellar furrow of similar depth; glabella with elongate, semi-elliptical outline, fairly strongly dorsally inflated in sagittal profile, not markedly raised above interocular fixigenae in anterior view, with dense tuberculate sculpture; tubercles somewhat finer than those on interocular fixigena and frontal area; S1 incised in smaller specimens as faint, strongly posteromedially directed furrow deepest at contact with axial furrow, effaced except as subtle 'notch' in larger specimens; S0 very short (sag., exsag.) and deeply incised; L0 long, longest medially, with sculpture of largest tubercles on cranium along posterior edge, fine tubercles on anterior part, confluent with posterior border, not obviously interrupted by axial furrow; posterior border shallow adaxially, but very deep along most of width; posterior border lengthening steadily abaxially, with sculpture of partially effaced but fairly large tubercles along posterior aspect; posterior fixigenae much less protruded laterally than in most hintzsecurines.

Libriginal field with width at midpoint of eye about 60% maximum length; field with substantial lateral convexity; eye relatively large, twice as long as wide; eye socle of very distinct but narrow single band, slightly wider anteriorly, set off from visual surface by shallow and narrow but distinctly inscribed furrow and from field by much deeper furrow; field with sculpture over most of surface of densely scattered small to moderate tubercles, more crowded than on frontal area of cranium; lateral border furrow shallow and quite broad, deepest anteriorly, field with smooth sector along furrow; posterior border furrow deep where cut by facial suture, but immediately shallowed toward base of genal spine; lateral border narrow, about same width as visual surface, with sculpture of subdued, partially effaced tubercles for the most part slightly smaller than those on field, and faint terrace lines on ventrolateral aspect, subparallel with lateral margin; posterior border shorter (exsag.) than width (tr.) of lateral border, lacking

sculpture; genal spine about 2/3 length of remainder of cheek excluding anterior projection, with subdued tubercles on proximal part but tapering rapidly and losing sculpture, with sharp point; genal spine nearly straight, with little posterior curvature; doublure reaching adaxial edge of ventral aspect of lateral border furrow, smooth and slightly concave, panderian notch absent.

Rostral plate not recovered. Hypostome and thorax not identified.

Pygidium with sagittal length (including articulating half-ring) 55% of maximum anterior width; axis occupying 40% of width anteriorly; axial furrow very narrow but firmly inscribed, shallowing posteriorly; axis with three distinct axial rings, third ring effaced along posterior aspect, grading into ill-defined terminal piece, rear of axis poorly defined except by break in slope in sagittal profile; axial rings lacking sculpture; pseudoarticulating half-rings present on second and third segments; ring furrows very short and deeply inscribed laterally, shallower and slightly bowed posteriorly medially; strong border of similar length/width developed around entire pygidium, with closely spaced subparallel terrace lines except on dorsal aspect; first pleural furrow well inscribed, deflected in course slightly at fulcrum, contacting inner edge of border; posterior interpleural and pleural furrows increasingly effaced, those of third segment not visible; pleural bands of first and second segments with minute, nearly effaced transverse rows of tubercles (best seen ventrally); posterior pleural band slightly longer (exsag.) than anterior band; posterior pleural band of first segment with large knob-like tubercle/spine immediately adjacent to axial furrow; smaller similar structure on second segment, about 1/4 the size of first, and minute ventral trace visible on third segment; posterior pygidial margin with strong median embayment; in posterior view, pleurae proximal to fulcrum held in horizontal plane, pleurae distal to fulcrum quite steeply declined, posteroventral margin with strong dorsal notch; doublure moderately narrow, of similar width everywhere, with sculpture of very fine terrace lines.

REMARKS. *Rossicurus lepidus* is the youngest member of the genus recovered from the Ibex sections. It differs from older undescribed species in the greater degree of transverse cephalic arching, stronger cranial vaulting, shorter genal spine with broader field, and entirely smooth pygidium with very strong knob-like tubercle on first segment.

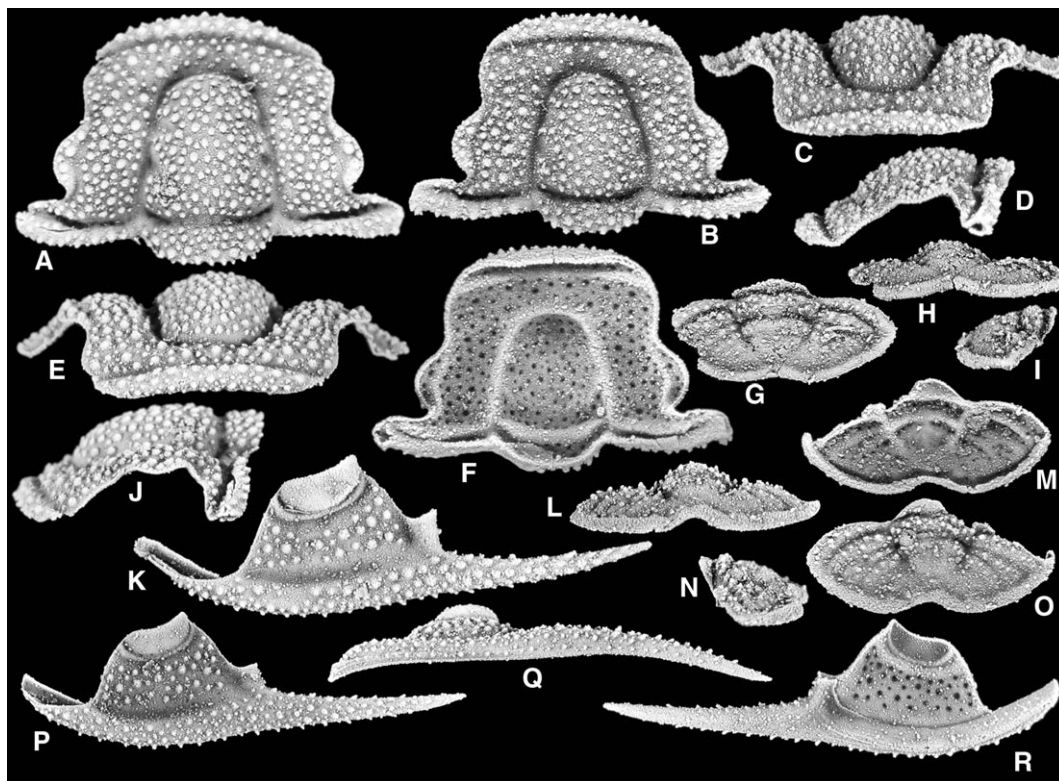


FIG. 9. *Genalaticurus genalatus* (Ross, 1951), from the Garden City Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Franklin Basin, section FB7 39.0-44.2m. A, E, J, cranidium, SUI 99581, dorsal, anterior and left lateral views, $\times 6$. B-D, F, cranidium, SUI 99582, dorsal, anterior, left lateral and ventral views, $\times 10$. G-I, pygidium, SUI 99583, dorsal, posterior and right lateral views, $\times 7.5$. K, left librigena, SUI 99584, external view, $\times 7.5$. L-O, pygidium, SUI 99585, posterior, ventral, left lateral and dorsal views, $\times 6$. P-R, left librigena, SUI 99586, external, ventrolateral and internal views, $\times 7.5$.

Genalaticurus gen. nov.

TYPE SPECIES. *Hystericurus genalatus* Ross, 1951, from the Garden City Formation, Ibexian (Skullrockian), Idaho.

OTHER SPECIES. *Genalaticurus* sp. nov. 1 (LDN 146.5m).

ETYMOLOGY. After the type species.

DIAGNOSIS. Cranidial sculpture dense, of distinctive flat-topped tubercles; very broad interocular fixigenae; anterior border strongly tuberculate along dorsal and posterior aspect; pygidium small, tuberculate, with a very strong posteromedian inflection.

REMARKS. *Genalaticurus* is compared with *Lavadamia*, the taxon it most resembles, under discussion of that genus below.

Genalaticurus genalatus (Ross, 1951) (Fig. 9)

Hystericurus genalatus Ross, 1951: 40, pl. 8, figs 1-13. Indefinitely assigned pygidia from zone 'B'; Ross, 1951: pl. 9, figs 12?, 18? [only].

MATERIAL AND OCCURRENCE. SUI 99581-99586 from Section FB7 39.0-44.2m, Garden City Formation, Franklin Basin, Bear River Range, southeastern Idaho. Also occurs at Section LDN 144.0-144.2m, Red Canyon Member, House Formation, southern House Range, Ibex area, Millard County, western Utah. All Skullrockian ('Zone B - *Bellefontia-Xenostegium* Zone').

DIAGNOSIS. As for genus.

DESCRIPTION. Cranidium (excluding posterior fixigenae) subquadrate in outline, with length about 80% of width across palpebral lobes; width across palpebral lobes slightly less than 80% of width across posterior fixigenae;

glabella gently tapered and rounded anteriorly, occupying about 75% of cranial length and about 40% of cranial width across palpebral lobes; convex, accounting for about 60% of cranial height in anterior view, but raised only slightly above adjacent portions of fixigenae; longitudinal profile of glabella arched very gently upward between occipital ring and point opposite mid-point of palpebral lobe, then curved gradually downward to preglabellar furrow; axial and preglabellar furrows well-incised grooves; occipital furrow firmly impressed, nearly transverse medially but curved gently forward towards axial furrow; occipital ring occupies about 20% of glabellar length; S1 and S2 expressed only near axial furrows as faint, oblique bands that lack sculpture; L1 about 140% length of occipital ring; L2 roughly length of occipital ring; frontal lobe about 30% of glabellar length; frontal area divided into gently inflated preglabellar field and convex, forwardly curved border by firmly impressed border furrow; border about 40% of frontal area length; gently curved palpebral lobe centred opposite S1 with length equal to slightly less than 40% of glabellar length; separated from fixigena by finely etched, arcuate palpebral furrow; palpebral ridge absent; palpebral region of fixigena broad, equal to about 50% of glabellar width at S1; slopes steeply upward from axial furrow to become gently inflated near, and raised slightly above, palpebral lobe; anterior sections of facial sutures very weakly divergent before swinging inward just behind anterior border furrow; posterior sections sharply divergent before curving backward near posterior border furrow, producing a faintly sigmoid course; posterior fixigenae with deep posterior border furrow; convex posterior border about 10% of glabellar length; surface of cranium with large rounded tubercles and scattered smaller tubercles; along posterior border and occipital ring, some tubercles spinose.

Librigena with gently curved genal spine, somewhat longer than librigenal field; field broad, subtrapezoidal, steeply upsloping; visual surface of eye mounted on wire-like eye socle; lateral and posterior borders broad, shallow and do not join; lateral border strongly convex, wide and tubular; posterior border shorter and gently convex; doublure extends inward as far as lateral and posterior border furrows; field with large, rounded tubercles augmented by scattered, smaller tubercles; tubercles on lateral border and genal spine pointed and weakly spinose; doublure with fine terrace ridges.

Pygidium transversely subelliptical, length equal to about 40% of width, with well-defined, narrow median embayment; weakly convex, with height in posterior view more than 25% of maximum width; gently tapered, posteriorly rounded axis weakly arched, occupies about 55% of pygidial height in posterior view; accounts for 75% of pygidial length and about 25% of maximum pygidial width; axial furrows very shallow grooves; at least on axial rings and terminal piece separated by shallow, weakly curved ring furrows; second, ill-defined axial ring on some specimens; short, arcuate articulating half ring; anteriormost axial ring about 30% of axis length; pleural field gently inflated near axial furrow, then flexed gradually downward towards border; two pairs of pleural and interpleural furrows; posterior and lateral borders narrow, weakly convex rims, merging with anteriormost pleural band; border furrow shallow but well-defined; pleural bands and axial rings with small rounded to pointed tubercles, borders smooth.

REMARKS. *Genalaticurus genalatus* is common through the uppermost Red Canyon Member of the House Formation. It is not, however, ubiquitous through its range. It is absent, for example, from horizon LDN 144m, which has yielded a rich sample of hintzecurines with which *G. genalatus* occurs at other horizons. *G. genalatus* is succeeded at LDN 146m by a subtly differentiated undescribed species.

Politicurus gen. nov.

TYPE SPECIES. *Hystricurus politus* Ross, 1951, from the Garden City Formation, Ibexian (Skullrockian), Idaho.

OTHER SPECIES. *Hystricurus?* sp. F of Ross (1951); at least five further undescribed effaced species and two undescribed strongly tuberculate species are present in the Red Canyon Member, House Formation, and the Garden City Formation.

ETYMOLOGY. After the type species.

DIAGNOSIS. Large for subfamily. Stout occipital spine on rear of L0 (reduced in large adults of undescribed, stratigraphically youngest species); usually dorsally effaced, with only subdued tubercles on frontal area and librigenal field; genal spine very long and strongly curved; pygidium long, nearly semicircular, posteromedian embayment not visible in dorsal view.

REMARKS. *Politicurus* is represented in the House and Garden City Formations by multiple

unnamed and undescribed species in addition to the type. The species form two groups, which may require generic subdivision. *Politicurus politus* represents the more diverse and abundant group (upon which the diagnosis above is based), species of which usually possess a stout occipital spine and either lack tuberculate sculpture or have only subdued sculpture restricted to the frontal areas and, in some species, the librigenal field. At least five new species of this group have thus far been identified. A second group is characterized by dense and abundant tuberculate sculpture over most of the cranidium and librigenal field, small spines flanking the short and slender medial occipital spine, and much greater transverse convexity of the anterior border. This group is represented in our collections by two undescribed species.

Politicurus is the largest hystricurid trilobite in all collections in which it occurs. Large pygidia are typical and until an articulated specimen (Fig. 11) was recovered, it was assumed that the genus was less micropygous than other hintzecurines. Instead, given that *P. politus* is quite strongly micropygous, it must have achieved a very large size. The largest pygidia recovered are nearly 1cm across. Given the proportions of the exoskeleton (Fig. 11), these individuals would have been around 14cm in length, excluding the posterior extent of the thoracic axial spine.

P. politus is certainly quite different from other hintzecurines, with its large, dorsally effaced exoskeleton, occipital spine, semicircular pygidium, and very long genal and thoracic axial spines. The strongly tuberculate species mentioned above, however, are intermediate in these features and much more closely resemble typical hintzecurines. There is little question that *Politicurus* is an effaced hintzecurine.

The only other species of *Politicurus* for which sclerites have been illustrated is '*Hystricurus* sp. F' of Ross (1951), which is probably conspecific with the specimens assigned by Hintze (1953, pl. 6, figs 7-1) to *P. politus*. As recognised by Ross, this species differs from *P. politus* in its much narrower palpebral lobes. In addition, it has a much more dorsally directed occipital spine with a more robust base. As one of Hintze's specimens (1953, pl. 6, fig 8) demonstrates, the occipital spine is also more than twice the length of that of *P. politus*. Undescribed species of *Politicurus* amongst the effaced group vary in cranial dimensions and dorsal convexity, thickness, length, and even presence of occipital spine, flexure of the librigena, length and curvature of the genal

spine, and dimensions and other features of the pygidium.

***Politicurus politus* (Ross, 1951)** (Figs 10,11)

Hystricurus? politus Ross, 1951: 45, pl. 9, figs 23,24,27,28,32,33, pl. 15, figs 1-6.
Indefinitely assigned pygidia from zone 'B'; Ross, 1951: pl. 9, fig. 1 [only].

MATERIAL AND OCCURRENCE. Topotypes SUI 99593-99597, from Section FB7 39.0-44.2m, Garden City Formation, Franklin Basin, Bear River Range, Franklin County, southeastern Idaho. SUI 99598, from Section LDN 144.0m, Red Canyon Member, House Formation, southern House Range, Ibex area, Millard County, western Utah. All Skullrockian ('Zone B - *Bellefontia-Xenostegium* Zone').

DIAGNOSIS. Cranidium only moderately vaulted; occipital spine slender and posteriorly directed; subdued tubercles present on frontal area and anterior part of librigenal field; palpebral lobes large, with well defined palpebral furrow; librigena strongly flexed, genal spine long and curved.

DESCRIPTION. Cranidium with sagittal length (excluding occipital spine) about 65% maximum width across posterior fixigenae; width across maximum point of divergence of anterior sections of facial sutures approx. 85% width across midpoint of palpebral lobes; glabella with sagittal length (in dorsal view) 75% length of cranidium excluding occipital spine; glabella anterior to S0 with maximum width across rear of L1 subequal to sagittal length; type and topotype specimens are somewhat flattened, but glabella with moderate sagittal convexity, describing arc with curvature significantly greater than that of cranidium in general; anterior border with steep posterior scarp along anterior border furrow, dorsally flattened along most of length (sag.; exsag.), and strongly curved, tubular in sagittal section anteriorly, similar in length sagittally and exsagittally (apparent reduction in exsagittal length is due to bisection by facial suture); anterior border strongly upturned relative to slope of frontal area, with relatively weak transverse flex in anterior view (though this could be muted by flattening); anterior border dorsally smooth; anterior border furrow short (sag.; exsag.) and deeply incised, nearly transverse but with faint 'W' shape in dorsal view, of similar depth along course; preglabellar field and frontal area with scattered tubercles, low and only faintly expressed in large holaspides, and very fine caecal pitting; preglabellar field with sagittal

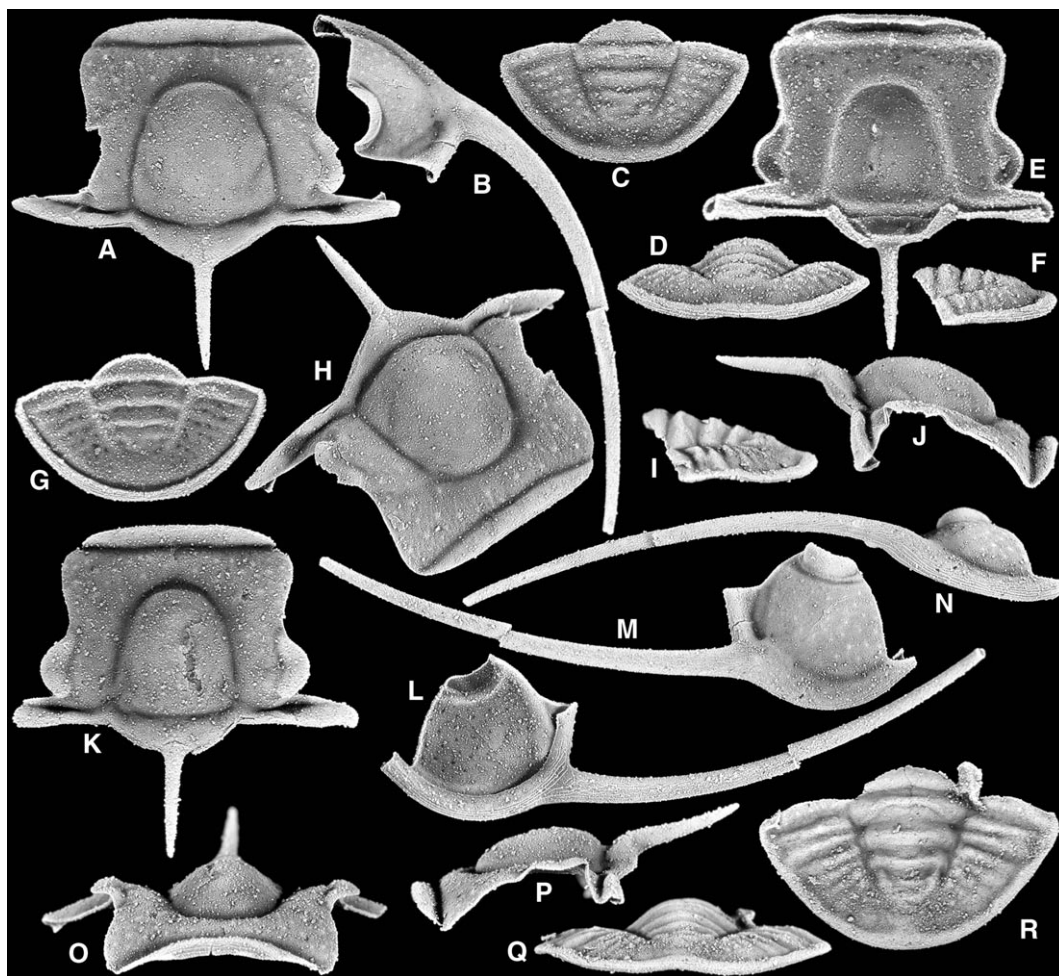


FIG. 10. A-R, *Politicurus politus* (Ross, 1951), from the Garden City Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Franklin Basin, section FB7 39.0-44.2m; topotype material. A, H, J, cranium, SUI 99593, dorsal, oblique and right lateral views, $\times 5$. B, L-N, right librigena, SUI 99594, dorsal, internal, external and ventrolateral views, $\times 5$. C, D, F, G, pygidium, SUI 99595, dorsal, posterior, left lateral and ventral views, $\times 7.5$. E, K, O, P, cranium, SUI 99596, ventral, dorsal, anterior and left lateral views, $\times 7.5$. I, Q, R, pygidium, SUI 99597, left lateral, posterior and dorsal views, $\times 7.5$.

length slightly greater than that of L0, strong dorsal convexity immediately anterior to prelabellar furrow, gentler and more even in slope anteriorly; anterior sections of facial suture moderately anteriorly divergent in front of palpebral lobe, widest divergence just behind anterior border furrow, strongly anteriorly convergent opposite anterior border furrow and anterior border; eye ridge faintly expressed to almost wholly effaced in large holaspides, running from junction of prelabellar and axial

furrow posterolaterally to front of palpebral lobe, with slight anterior curvature; interocular fixigena broad, lacking dorsal sculpture, gently inclined toward glabella; palpebral furrow shallow but perceptibly incised along its length, describing sinuous 'W' shape; palpebral lobe relatively large, kidney-shaped, lacking dorsal sculpture, set in horizontal plane, lateral outline nearly semicircular in dorsal view; glabella bullet-shaped in dorsal outline, axial furrows laterally bowed and gently anteriorly convergent,

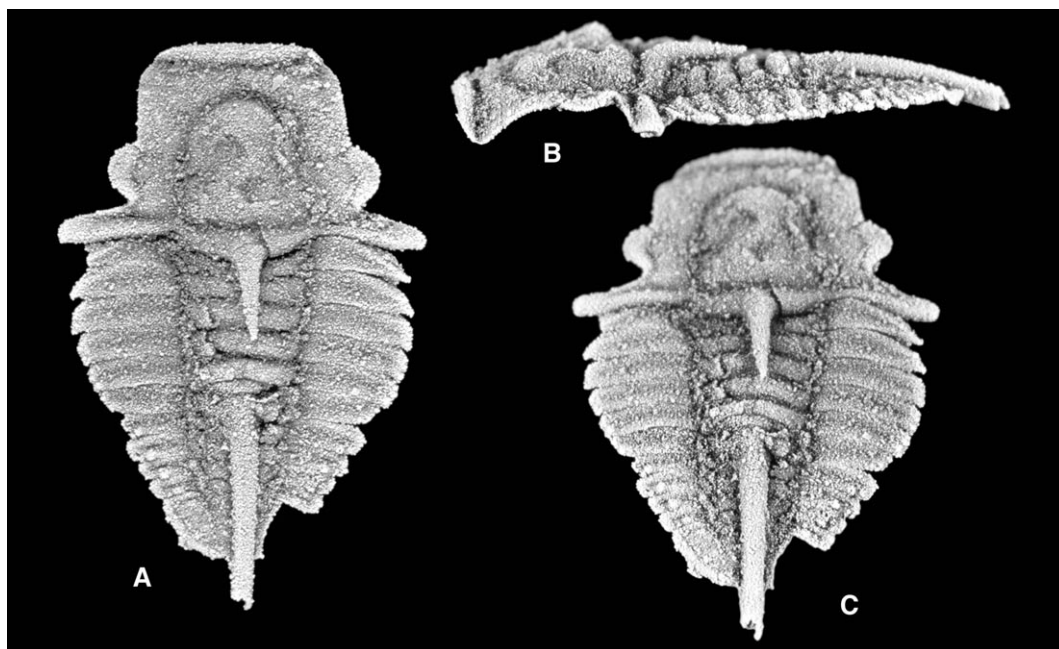


FIG. 11. *Politicurus politus* (Ross, 1951), from the Red Canyon Member, House Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Ibex area, section Lava Dam North 144.0m. A-C, articulated individual lacking librigenae, SUI 99598, dorsal, left lateral and dorsal pygidial views, $\times 10$.

running without interruption into preglabellar furrow; occipital, axial, and preglabellar furrow similar in length/width and depth, narrowly incised; preglabellar furrow anteriorly arcuate; glabellar furrows very weakly expressed, only S1 discernible on all large specimens; glabella lacking dorsal sculpture; posterior fixigena slightly swollen and dorsally convex opposite L1, running into very short (exsag.) strip abaxially in front of posterior border; L0 lacking dorsal sculpture, longer medially than laterally; occipital spine with base set at rear of L0, 40–45% sagittal length of remainder of cranidium, slender, tapering distally to point, elevated slightly above horizontal plane, tip curved gently dorsally; posterior border running nearly exactly transversely, contiguous with L0 (not interrupted by axial furrow), longer distally (past fulcrum) than proximally, tubular in section, lacking dorsal sculpture; posterior border furrow running from tripartite junction with axial and occipital furrows, very short and incised, markedly deeper in front of fulcrum; doublure beneath posterior border short (exsag.) proximally, considerably longer distally.

Librigena with field very broad and convex;

entire librigena flexed, describing more or less smooth arc in posterolateral view; eye relatively small and narrow (tr.); eye socle of very thin and subdued single band, set off from eye and field by very narrow furrows; field mostly smooth, with widely scattered and very subdued tubercles on anterior part only; lateral border furrow shallow but narrow and with distinct course; lateral border furrow and lateral border with strong lateral convexity; posterior border furrow deeper than lateral border furrow; posterior and lateral border furrows do not meet, but end at broad shallow area in front of genal spine base; lateral border tubular, broader posteriorly, with sculpture of extremely fine terrace lines on lateral and ventrolateral aspect; genal spine extremely long, strongly curved, tapering to sharp point; doublure quite narrow, with very distinct sculpture of terrace lines running subparallel to margins, continued posteriorly along proximal-ventral aspect of genal spine, panderian notch absent.

Hypostome not identified.

Thorax of 10 segments, with large axial spine on sixth; first segment narrower than width of cranidial posterior fixigenae; second segment

wider and third segment widest, nearly but not quite as wide as posterior fixigenae; segments 4-6 narrow rapidly, segments 7-10 also progressively narrower, but not narrowing as rapidly as 4-6; in general, segments are long (sag., exsag.) and lack dense or scattered tuberculate sculpture; segments 1-6 lack tuberculate sculpture except for pleural tips; segments 7-10 bear a single prominent tubercle on distal part of posterior pleural band; segments 1 and 2 have a single short, posteriorly directed spine at pleural tip; segments 3-10 have a pair of very short spines/tubercles at pleural tips; axis occupying 40% of thoracic width across segment 1, 34% across segment 3, 35% across segment 6, and 45% across segment 10; axial furrows shallow; pleural furrows very shallow and long anteriorly, more furrow-like and circumscribed on posterior segments; anterior pleural band ridge-like distally on first two segments to accommodate large articular facet; anterior and posterior pleural bands not well defined on segments 1-6; pleurae with distinct marginal border matching that of pygidium on segments 7-10; axial rings smooth; robust, smooth median spine developed on sixth axial ring, length in articulated specimen not known with certainty, but isolated segments (not figured) show that spine was very long and extended posteriorly well past rear of pygidium.

Pygidium long, broadly semicircular; sagittal length 55-60% width; posterior margin smoothly arcuate and semicircular, with gentle median dorsal inflection in posterior view; border of similar width developed around entire pygidium, with dorsal sculpture of fine terrace lines; axis occupying 40% maximum pygidial width anteriorly; axial furrows nearly straight, shallow but well inscribed, posteriorly convergent, effaced posteromedially but more or less fully circumscribing rear of axis; three distinct axial rings, faint fourth not fully differentiated from terminal piece; ring furrows deep, similar depth across width; very prominent pseudoarticulating half ring on second segment, smaller on third; axial rings lack dorsal sculpture; faint muscle impression discernible on lateral aspect of at least first and second rings; pleural and interpleural furrows vary in degree of expression among specimens, typically first pleural furrow quite strong and posterior furrows increasingly effaced; anterior and posterior pleural bands similar in length; most specimens with scattered but subdued fine tuberculate sculpture over most of pleural area, but some nearly lack tubercles; doublure relatively narrow, and of similar width

everywhere, with sculpture of very fine, closeset terrace lines.

REMARKS. *Politicurus politus* occurs in the Garden City and House Formations. It is the second youngest species known, and bears a relatively slender and short occipital spine compared to most older species.

Lavadamia gen. nov.

TYPE SPECIES. *Lavadamia joplinae*, from the House Formation, Ibexian (Skullrockian), Utah.

OTHER SPECIES. Monotypic.

ETYMOLOGY. After 'Lava Dam', the weathered Tertiary lava flow from which section Lava Dam North takes its name.

DIAGNOSIS. Glabella relatively small, not strongly inflated, and subtriangular; palpebral lobes large and set posteriorly; occipital ring shelf-like, with 4-7 prominent short spines running posteriorly from posterior margin; librigenal field relatively small, mostly lacking sculpture; genal spine very long; pygidium apparently much smaller relative to cranidium than any other member of subfamily, with only 2 discernible segments and nearly lacking in dorsal sculpture.

REMARKS. The striking morphology of this species is not matched by that of any other hintzecurine. The options are to classify it in a taxon of convenience or to erect a monotypic genus. Since it seems clear that the species is not an ingroup member of any of the clades recognised as new hintzecurine genera herein, it seems preferable to erect a new genus. Of other hintzecurines, *Hintzecurus paragenalatus* has genal spines of similar length. Early species of *Hintzecurus* (undescribed) do not have long genal spines, however, and the spine length almost certainly evolved independently within *Hintzecurus*. *Hintzecurus* is not otherwise closely comparable to *Lavadamia joplinae*. *Genalaticurus* is perhaps the most similar taxon, with comparable cranial dimensions, incision of glabellar furrows, and most nearly approaching the subtriangular glabellar shape of *Lavadamia*. The pygidium of *Genalaticurus* is also relatively small, though not nearly so much as that of *Lavadamia*. In other features the genera are less similar: *Genalaticurus* has narrow palpebral lobes more typical of other members of the subfamily, is densely tuberculate over the entire cephalon, and has a librigena that does not

resemble that of *Lavadamia*, with broad tuberculate field, deeper lateral border furrow, and short, tuberculate genal spine. Most obviously, *Genalaticurus* lacks the prominent posterior occipital spine row characteristic of *Lavadamia*. It is possible that *Lavadamia* and *Genalaticurus* are sister taxa.

***Lavadamia joplinae* sp. nov.**
(Fig. 12)

ETYMOLOGY. After Janis Joplin.

MATERIAL AND OCCURRENCE. Holotype SUI 99587 and paratypes SUI 99588-99592, from Section LDN 142.6m, Skullrockian ('Zone B - *Bellefontia-Xenostegium* Zone'), Red Canyon Member, House Formation, southern House Range, Millard County, western Utah. Known only from the type horizon.

DIAGNOSIS. As for genus.

DESCRIPTION. Cranium with sagittal length 67% width; width across midpoint of palpebral lobes 80% width; glabella occupying 80% of sagittal length of cranium; glabella with maximum width across rear of L1 90% sagittal length (excluding L0); anterior margin gently and evenly arched; anterior border with nearly flat dorsal aspect, sharp break in slope at about midlength, and anterior aspect that is slightly anteriorly convex in sagittal profile; anterior border lacking sculpture on rear half, with fairly densely scattered fine tubercles on anterior aspect; anterior border furrow relatively long and shallow for subfamily; anterior border and border furrow of similar length (sag., exsag.); anterior sections of facial sutures bowed laterally, maximum point of divergence opposite rear third of preglabellar field; palpebral lobes posteriorly set for subfamily, large, length (exsag.) 30% sagittal cranial length, held in horizontal plane in anterior view, broad and crescentic, with sculpture of closely scattered but subdued small tubercles; palpebral furrow not strongly impressed but distinct, sharp break in slope at adaxial edge of crescentic palpebral lobe, furrow bowed laterally to run subparallel to lateral margin of lobe; preglabellar field about 130% length (sag.) of anterior border, with only slight dorsal inflation in sagittal profile; preglabellar field and anterior frontal areas with very subdued sculpture of nearly effaced small tubercles; interocular fixigena broad, dorsally convex in transverse profile, sloping more toward glabella than palpebral lobe, with sculpture of densely packed medium tubercles much larger and more crowded than on frontal area; posterior fixigena

very limited in extent, extremely short (exsag.) strip in front of posterior border furrow; axial furrows straight and quite strongly anteriorly convergent, running into strongly arched preglabellar furrow to circumscribe subtriangular glabella; axial furrow shallower on posterior half than anterior half; S1 discernible in large specimens, running strongly posteromedially toward S0, not well impressed, defining small, subdued triangular L1, indistinct in some specimens; S2 subtle notch; glabella weakly inflated, with sculpture of dense moderate tubercles on rear 3/4, similar to that of interocular fixigena, tubercles effaced from anterior lobe; L0 long, inclined dorsally, lacking sculpture over most of surface, with 4-7 prominent but short, posteriorly-directed spines running from posterior margin, very small tubercle or tubercles in posteromedian area; S0 similar in depth to axial furrow, deeper laterally in some specimens, of uniform depth in others; axial, occipital, and posterior border furrows meeting at tripartite junction, only slightly shallowed; posterior border furrow deep, short (exsag.); posterior border tubular, with 1 or 2 subdued tubercles on adaxial part, lengthening (exsag.) abaxially.

Librigenal field with width at midlength of eye 35% exsagittal length, smooth and devoid of sculpture except for subdued tubercles on posterior part along posterior section of facial suture in smaller specimens; visual surface very convex; eye socle of very narrow but distinct single band, set off from visual surface and field by very narrow inscribed furrows of similar depth; posterior and lateral border furrows very shallow; lateral border narrow, with sculpture of densely crowded, fine, and subdued tubercles similar to that on anterior aspect of cranial anterior border; genal spine very long, tapering gradually to sharp point, with fine dorsomedian furrow and faint tubercles carried along from lateral border for short distance from base on lateral aspect of spine; doublure broad, reaching base of field, with sculpture of very fine terrace lines.

Rostral plate, hypostome, and thorax not identified.

Pygidium small, sagittal length 45% width; maximum width of axis 30% pygidial width; prominent fairly broad border and distinct but shallow border furrow; posterior margin arcuate in plan view for most of course, deflected anteriorly and dorsally in median embayment; axial furrow shallow, not meeting to fully circumscribe axis posteriorly; 2 axial rings

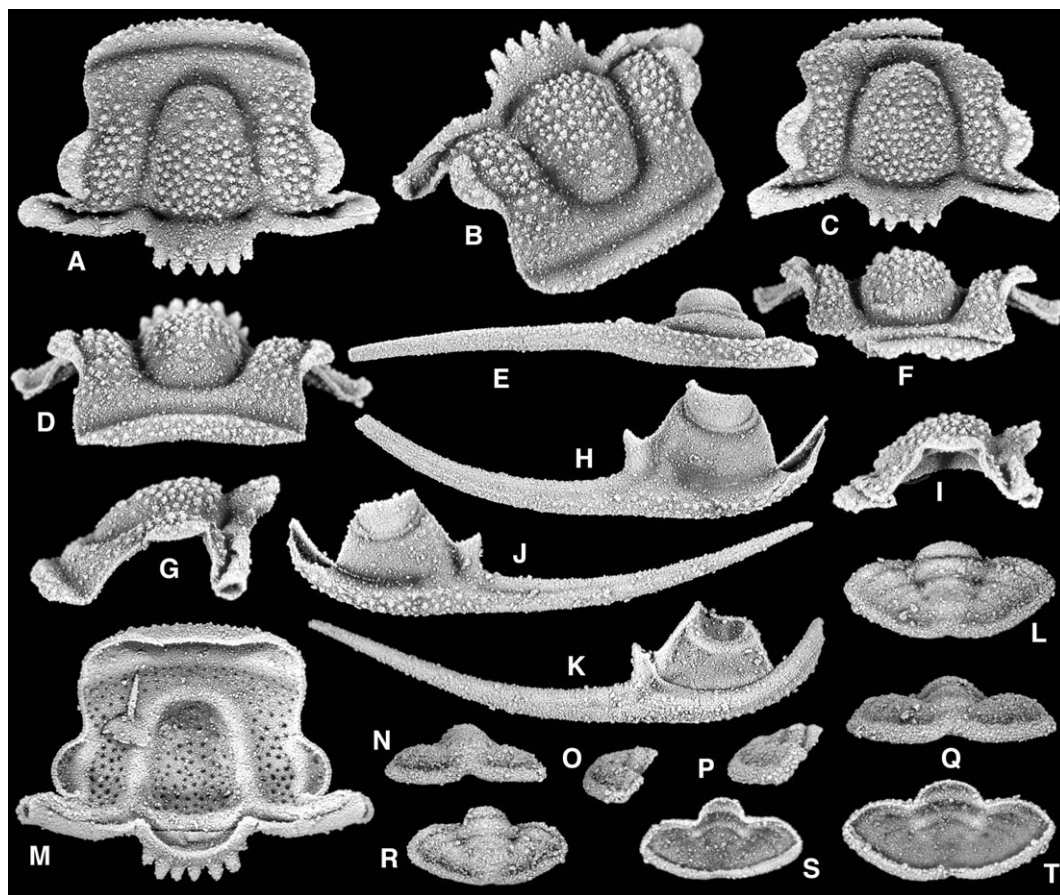


FIG. 12. *Lavadamia joplinae* gen. et sp. nov., from the Red Canyon Member, House Formation (Skullrockian, *Bellefontia-Xenostegium* Zone), Ibex area, section Lava Dam North 142.6 m. A, B, D, G, M, cranidium, holotype, SUI 99587, dorsal, oblique, anterior, left lateral and ventral views, $\times 7.5$ (structure on upper left quadrant of M is a small asaphid transitory pygidium attached to specimen). C, F, I, cranidium, SUI 99588, dorsal, anterior and left lateral views, $\times 7.5$. E, H, right librigena, SUI 99589, ventrolateral and external views, $\times 6$. J, K, left librigena, SUI 99590, external and internal views, $\times 7.5$. L, P, Q, T, pygidium, SUI 99591, dorsal, right lateral, posterior and ventral views, $\times 10$. N, O, R, S, pygidium, SUI 99592, posterior, right lateral, dorsal and ventral views, $\times 10$.

discernible, second one partially effaced, terminal piece with structure largely effaced; first ring furrow inscribed along course, much deeper laterally; second ring furrow effaced medially; first and second pleural and interpleural furrows discernible, becoming progressively effaced posteriorly; posterior pleural band longer (exsag.) than anterior band; pygidium lacking dorsal sculpture except for minute tubercles on pleural bands of first segment; doublure relatively narrow.

REMARKS. *Lavadamia joplinae* is common at LDN 142.6m, but does not occur at any other horizon in the Lava Dam North section. At Middle Mountain, it is very common at MME 0.6m, but again restricted to a single horizon. Uniquely among the new hintzcurine genera in the *Politurus* Interval, it has not been recovered from the Garden City Formation.

ACKNOWLEDGEMENTS

J.M.A. and S.R.W.'s research was supported by NSF grant EAR 9973065. B.D.E.C. and D.-C. Lee's research was supported by a Natural

Sciences and Engineering Research Council of Canada operating grant to B.D.E.C. We are grateful to D. Schultz, J. Forish, and T. McCormick for assistance in the field.

LITERATURE CITED

- ADRIN, J.M., WESTROP, S.R., LANDING, E. & FORTEY, R.A. 2001. Systematics of the Ordovician trilobites *Ischyrotoma* and *Dimeropygiella*, with species from the type Ibexian area, western U.S.A. *Journal of Paleontology* 75: 947-971.
- ANGELIN, N.P. 1854. *Palaeontologica Scandinavica. Pars II, Crustacea formationis transitionis. (Academiae Regiae Scientiarum Suecanae: Holmiae)* 25-92.
- ANTSYGIN, N.Ya. 1978. [Early Ordovician trilobites from the Mayachnaya Mountain in the Vredinsk district]. *Trudy Instituta Geologii i Geokhimii, Akademiya Nauk SSSR, Ural'skiy Nauchnyy Tsentr* 135: 30-44.
- APOLLONOV, M.K. & CHUGAEVA, M.N. 1983. [Some trilobites from the Cambrian and Ordovician boundary deposits of Batyrbai Gorge in Malyy Karatau]. Pp. 66-90. In Apollonov, M.K., Bandaletov, S.M. & Ivshin, N.K. (eds) [The Lower Palaeozoic stratigraphy and paleontology of Kazakhstan]. (Nauka, Kazakh SSR Publishing House: Alma-Ata).
- BERG, R.R. & ROSS, R.J., Jr 1959. Trilobites from the Peerless and Manitou formations, Colorado. *Journal of Paleontology* 33: 106-119.
- BILLINGS, E. 1859. Description of some new species of trilobites from the Lower and Middle Silurian rocks of Canada. *Canadian Naturalist and Geologist* 4: 367-383.
- BOYCE, W.D. 1989. Early Ordovician trilobite faunas of the Boat Harbour and Catoche Formations (St. George Group) in the Boat Harbour-Cape Norman area, Great Northern Peninsula, western Newfoundland. Newfoundland Department of Mines and Energy, Geological Survey Branch, Report 89-2: 1-169.
- BRIDGE, J. & CLOUD, P.E., Jr 1947. New gastropods and trilobites critical in the correlation of Lower Ordovician rocks. *American Journal of Science* 245: 545-559.
- BURSKII, A.Z. 1970. [Early Ordovician trilobites of central Pai-Khoya]. Pp. 96-138. In Bondareva, V.N. (ed.) [Reference papers on the Ordovician in Pai Khoya, Vaigach Islands and S. Novaya Zemlya]. (Nauchno-Issledovatel'skiy Institut Geologii Arktiki, Ministerstva Geologii SSSR: Leningrad). (in Russian)
- CHUGAEVA, M.N. 1962. [A new Early Ordovician genus of the subfamily Hystricurinae from the Kolyma basin]. *Paleontologicheskij Zhurnal* 3: 61-64. (in Russian)
- CULLISON, J.S. 1944. The stratigraphy of some Lower Ordovician formations of the Ozark uplift. *Bulletin of the School of Mines and Metallurgy, University of Missouri, Technical Series* 15(2): 1-112.
- DESBIENS, S., BOLTON, T.E. & MCCracken, A.D. 1996. Fauna of the lower Beauharnois Formation (Beekmantown Group, Lower Ordovician), Grande-Île, Quebec. *Canadian Journal of Earth Sciences* 33: 1132-1153.
- ETHINGTON, R.L. 1978. Conodont faunas of the Lower and Middle Ordovician of the House and Confusion Ranges, Utah. Pp. 35-44. In Miller, J.F. (ed.) *Southwest Missouri State University, Science Series* 5.
- ETHINGTON, R.L. & CLARK, D.L. 1981. Lower and Middle Ordovician conodonts from the Ibex area, western Millard County, Utah. *Brigham Young University Geology Studies* 28(2): 1-155.
- FORTEY, R.A. 1990. Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* 33: 529-576.
- FORTEY, R.A. & HUGHES, N.C. 1998. Brood pouches in trilobites. *Journal of Paleontology* 72: 638-649.
- FORTEY, R.A. & OWENS, R.M. 1975. Proetida – a new order of trilobites. *Fossils and Strata* 4: 227-239.
- FORTEY, R.A. & OWENS, R.M. 1990. Trilobites. Pp. 121-142. In McNamara, K.J. (ed.) *Evolutionary Trends*. (Belhaven Press: London).
- GOBBETT, D.J. 1960. A new species of trilobite from the Lower Oslobreen Limestone. *Geological Magazine* 107: 457-459.
- HELLER, R.L. 1956. Stratigraphy and paleontology of the Roubidoux Formation of Missouri. *Missouri Geological Survey and Water Resources, Series* 2 35: 1-113. (for 1954)
- HINTZE, L.F. 1951. Lower Ordovician detailed stratigraphic sections for western Utah. *Utah Geological and Mineralogical Survey Bulletin* 39: 1-99.
1953. Lower Ordovician trilobites from western Utah and eastern Nevada. *Utah Geological and Mineralogical Survey Bulletin* 48: 1-249. (for 1952)
1973. Lower and Middle Ordovician stratigraphic sections in the Ibex area, Millard County, Utah. *Brigham Young University Geology Studies* 20: 3-36.
- HINTZE, L.F., TAYLOR, M.E. & MILLER, J.F. 1988. Upper Cambrian-Lower Ordovician Notch Peak Formation in western Utah. *United States Geological Survey Professional Paper* 1393: 1-30.
- HUPÉ, P. 1953. *Classe des Trilobites*. Pp. 44-246. In Piveteau, J. (ed.) *Traité de Paléontologie* 3.
- JELL, P.A. 1985. Tremadoc trilobites of the Digger Island Formation, Waratah Bay, Victoria. *Memoirs of the Museum of Victoria* 46: 53-88.
- JELL, P.A. & ADRIN, J.M. this volume. Available generic names for trilobites. *Memoirs of the Queensland Museum* 48(2): 331-551.
- JELL, P.A. & STAIT, B. 1985a. Tremadoc trilobites from the Florentine Valley Formation, Tim Shea

- Area, Tasmania. *Memoirs of the Museum of Victoria* 46: 1-34.
- JELL, P.A. & STAIT, B. 1985b. Revision of an early Arenig trilobite faunule from the Caroline Creek Sandstone, near Latrobe, Tasmania. *Memoirs of the Museum of Victoria* 46: 35-51.
- KHALFIN, L.L. (ed.) 1960. [Palaeozoic biostratigraphy of the Sayan-Altai mountain region. Part 1: Lower Palaeozoic, Cambrian System]. *Trudy Sibirskogo Nauchno-Issledovatel'skogo Instituta Geologii, Geofiziki i Mineral'nogo Syr'ya* 19: 11-253.
- KOBAYASHI, T. 1940. Lower Ordovician fossils from Caroline Creek, near Latrobe, Mersey River district, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 1939: 67-76. (for 1939)
- KOBAYASHI, T. 1955. The Ordovician fossils of the McKay Group in British Columbia western Canada, with a note on the early Ordovician palaeogeography. *Journal of the Faculty of Science, Tokyo University, Section 2* 9: 355-493.
- LEE, D.-C. & CHATTERTON, B.D.E. 1997. Hystericurid trilobite larvae from the Garden City Formation (Lower Ordovician) of Idaho and their phylogenetic implications. *Journal of Paleontology* 71: 862-877.
- LOCH, J.D., STITT, J.H. & MILLER, J.F. 1999. Trilobite biostratigraphy through the Cambrian-Ordovician boundary interval at Lawson Cove, Ibex, western Utah, U.S.A. Pp. 13-16. In *Quo vadis Ordovician - Short papers of the Eighth International Symposium on the Ordovician System. Acta Universitatis Carolinae, Geologica* 43.
- LOCHMAN, C. 1965. Lower Ordovician (Zone D) faunules from the Williston Basin, Montana. *Journal of Paleontology* 39: 466-486.
- LU, Y.-H. & ZHOU, T.-R. 1990. Trilobites across the Cambrian-Ordovician boundary of the transitional region of Sandu, southeastern Guizhou. *Palaeontologia Cathayana* 5: 1-84.
- MERGL, M. 1984. Fauna of the Upper Tremadoc of central Bohemia. *Sborník Geologických Ved. Paleontologie* 26: 9-46.
1994. Trilobite fauna from the Třenice Formation (Tremadoc) in central Bohemia. *Folia Musei Rerum Naturalium Bohemiae Occidentalis. Ser. Geologica* 3: 1-31.
- MILLER, J.F., EVANS, K.R., LOCH, J.D., ETHINGTON, R.L. & STITT, J.H. 2001. New lithostratigraphic units in the Notch Peak and House formations (Cambrian-Ordovician), Ibex area, western Millard County, Utah. *Brigham Young University Geology Studies* 46: 35-69.
- MILLER, J.F., TAYLOR, M.E., STITT, J.H., ETHINGTON, R.L., HINTZE, L.F. & TAYLOR, J.F. 1982. Potential Cambrian-Ordovician boundary stratotype sections in the western United States. Pp. 155-180. In Bassett, M.G. & Dean, W.T. (eds) *The Cambrian-Ordovician boundary: sections, fossils distributions, and correlations. National Museum of Wales, Geological Series* 3.
- NOLAN, T.B., MERRIAM, C.W. & WILLIAMS, J.S. 1956. The stratigraphic section in the vicinity of Eureka, Nevada. *United States Geological Survey Professional Paper* 276: 1-77.
- ÖPIK, A.A. 1967. The Mindyallen fauna of north-western Queensland. *Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin* 74: vol 1: 404 p. vol. 2: 167 p.
1970. Nepeid trilobites of the Middle Cambrian of northern Australia. *Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin* 113: 1-48.
- PENG, S.-C. 1984. Cambrian-Ordovician boundary in the Cili-Taoyuan border area, northwestern Hunan, with descriptions of relative trilobites. Pp. 285-404. In *Stratigraphy and Palaeontology of Systemic Boundaries in China. Cambrian-Ordovician Boundary. Vol. 1. (Anhui Science and Technology Press: Hefei)*.
1990. Tremadoc stratigraphy and trilobite faunas of northwestern Hunan. 2. Trilobites from the Panjiazui Formation and the Madaoyu Formation in Jiangnan Slope Belt. *Beringeria* 2: 55-171.
- PETRUNINA, Z.E. 1973. Novye rody i vidy tremadokskikh trilobitov Zapadnoi Sibiri. Pp. 59-71. In *Novye dannye po geologii i poleznym iskopaemym Zapadnoi Sibiri. (Izd-vo Tomskogo Universiteta, 8: Tomsk)*. (in Russian)
- POPOV, L.E., HOLMER, L.E. & MILLER, J.F. 2002. Lingulate brachiopods from the Cambrian-Ordovician boundary beds of Utah. *Journal of Paleontology* 76: 211-228.
- POULSEN, C. 1927. The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddelelser om Grønland* 70: 235-343.
- PŘIBYL, A. 1950. Re-naming some homonymic names of Bohemian and foreign trilobite genera. *Sborník Státního Geologického Ústavu Československé Republiky* 17: 193-200. (in Czech with English summary)
- RAYMOND, P.E. 1913. A revision of the species which have been referred to the genus *Bathyurus*. *Bulletin of the the Victoria Memorial Museum* 1: 51-69.
- ROSS, R.J., Jr 1951. Stratigraphy of the Garden City Formation in northeastern Utah, and its trilobite faunas. *Peabody Museum of Natural History, Yale University, Bulletin* 6: 1-161.
1953. Additional Garden City (Early Ordovician) trilobites. *Journal of Paleontology* 27: 633-646.
1965. Early Ordovician trilobites from the Seward Peninsula, Alaska. *Journal of Paleontology* 39: 17-20.
- ROSS, R.J., Jr, HINTZE, L.F., ETHINGTON, R.L., MILLER, J.F., TAYLOR, M.E. & REPETSKI, J.E. 1997. The Ibexian, lowermost series in the North American Ordovician. *United States Geological Survey Professional Paper* 1579: 1-50.

- ROZOVA, A.V. 1963. [Biostratigraphic scheme for subdividing Upper and upper part of Middle Cambrian of northwestern Siberian platform and new Upper Cambrian trilobites of the River Kulyumbe area]. *Geologiya i Geofizika* 1963(9).
- SHERGOLD, J.H. 1972. Late Upper Cambrian trilobites from the Gola Beds, western Queensland. Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin 112: 1-89. (for 1971)
- STITT, J.H. 1983. Trilobites, biostratigraphy, and lithostratigraphy of the McKenzie Hill Limestone (Lower Ordovician), Wichita and Arbuckle Mountains, Oklahoma. *Oklahoma Geological Survey Bulletin* 134: 1-54.
- TAYLOR, M.E. & LANDING, E. 1982. Biostratigraphy of the Cambrian-Ordovician transition in the Bear River Range, Utah and Idaho, western United States. Pp. 181-191. In Bassett, M.G. & Dean, W.T. (eds) *The Cambrian-Ordovician boundary: sections, fossil distributions, and correlations*. National Museum of Wales, Geological Series 3.
- VANĚK, J. 1965. Die Trilobiten des mittelhöhmischen Tremadoc. *Senckenbergiana lethaea* 46: 263-308.
- WALCOTT, C.D. 1886. Second contribution to the studies on the Cambrian faunas of North America. *United States Geological Survey Bulletin* 30: 1-369.
- WEBER, V.N. 1948. Trilobity silurijskich otlozenij SSR. 1. Niznesiluriskije trilobity. Monografii po Paleontologii SSSR 69: 1-111. (in Russian)
- WINSTON, D. & NICHOLLS, H. 1967. Late Cambrian and early Ordovician faunas from the Wilberns Formation of central Texas. *Journal of Paleontology* 41: 66-96.
- YIN, G.-Z. & LI, S. 1978. [Trilobita]. Pp. 385-595. In [Palaeontological Atlas of Southwest China. Guizhou Province. I. Cambrian-Devonian]. (Geological Publishing House: Beijing).
- ZHOU, T.-M., LIU, Y.-R., MENG, X.-S. & SUN, Z.-H. 1977. [Trilobita]. Pp. 104-266. In [Palaeontological Atlas of Central and South China. I. Early Palaeozoic]. (Geological Publishing House: Beijing).
- ZHOU, Z.-Y. & FORTEY, R.A. 1986. Ordovician trilobites from north and northeastern China. *Palaeontographica Abteilung A* 192: 157-210.