

The Carboniferous conodont *Lochriea commutata* (Branson and Mehl, 1941), the type species of *Lochriea* Scott, 1942: nomenclatural history, apparatus composition and effects on *Lochriea* species

Peter H. von Bitter,^{1*}  Rodney D. Norby,² and Robert G. Stamm³

¹Palaeobiology Section, Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6, Canada
<peter.vonbitter@sympatico.ca>

²Illinois State Geological Survey, Champaign, Illinois 61820, USA <rmorby@illinois.edu>

³U.S. Geological Survey, Reston, Virginia 20192, USA <rstamm@usgs.gov>

Abstract.—*Lochriea commutata* (Branson and Mehl, 1941), a senior subjective synonym of *Lochriea montanaensis* Scott, 1942, is the type species of *Lochriea* Scott, 1942, one of the first conodont genera named using bedding-plane assemblages. *Lochriea commutata* is both wide- and long-ranging, locally stratigraphically important, and a consistently recognized Carboniferous species, despite its taxonomic journey from *Spathognathodus* to *Gnathodus* to *Paragnathodus* to *Lochriea*.

Lochriea commutata was, as *Lochriea montanaensis*, initially reported to contain 22+ elements, the apparatus composition of the genus being subsequently amended to 17+ elements based on *Lochriea wellsii* Melton and Scott, 1973, which is an untenable hypothesis because the latter was a conodontophage. Restudy of original and new bedding-plane assemblages in the mid 1970s established that the first assemblages studied were fecal, the initial reconstruction incorporated elements of two individuals, and *Lochriea commutata* possessed a feeding apparatus of 2P₁, 2P₂, 2M, 2S₁, 2S₂, 2S₃, 2S₄, and 1S₀ elements. A *Lochriea* sp. bedding-plane assemblage was subsequently found to have the same element composition, and restudy of type material, available bedding-plane assemblages, and new fused clusters confirms that *Lochriea commutata* had a 15-element ozarkodinid apparatus.

While species are still assigned to *Lochriea* using carminiscaphate P₁ elements almost exclusively, those assignments must be considered tentative until their apparatuses are determined to be similar to that of *L. commutata*, and until characteristics of elements other than the P₁ element, particularly the makellate M element and the bipennate S_{3/4} element, are also taken into account.

Lochriea bigsnowyensis Scott, 1942 is reassigned to *Cavusgnathus* Harris and Hollingsworth, 1933.

Introduction

Subsequent to Norby (1976) restudying the type specimens of *Lochriea montanaensis* Scott, 1942 (Fig. 1) and describing newly collected bedding-plane assemblages of *Lochriea commutatus* (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]), several of which we refigure (Fig. 2), the conodont genus *Lochriea* Scott, 1942 was used to accommodate an increasing number of species and the biostratigraphic zones they define, with only minimal taxonomic and historical underpinnings that led to this usage ever having been presented. Despite assurances (Sweet, 1988, p. 111) that “species of . . . *Lochriea* . . . are represented by bedding-plane assemblages, hence there are few mysteries about [their] skeletal anatomy,” *Lochriea* and its apparatus were not nearly as well known then and in the intervening years as Sweet implied. Thus, we provide the foundations and justifications for accommodating certain Carboniferous carminiscaphate P₁ conodonts with unornamented or ornamented platforms, and

the elements they were biologically associated with, in the genus *Lochriea* instead of in other genera, including *Spathognathodus*, *Gnathodus*, and *Paragnathodus*. We do so by tracing the generic assignments of the P₁ elements of *Lochriea commutata* and related species, and by re-examining and documenting the element composition, and the number of elements in the apparatus of the type species of the genus *Lochriea*, *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b).

Range and biostratigraphic utility of *Lochriea*

The genus *Lochriea* occurs in, and is restricted to, strata of Carboniferous age. Atakul-Özdemir et al. (2012) concluded that the genus is monophyletic, biostratigraphically important, and that the first appearances of *Lochriea* species, and their transitions, are markers for global correlation (aspects of the latter were discussed by Somerville, 2008). *Lochriea commutata* and other species of *Lochriea* (some early listings were under the generic names *Gnathodus* and *Paragnathodus*) first appear at the base of the Viséan in Europe (Higgins, 1981), in the Arundian of England (Metcalf, 1981; Stone, 1991), in the lower Meramecian of

*Corresponding author

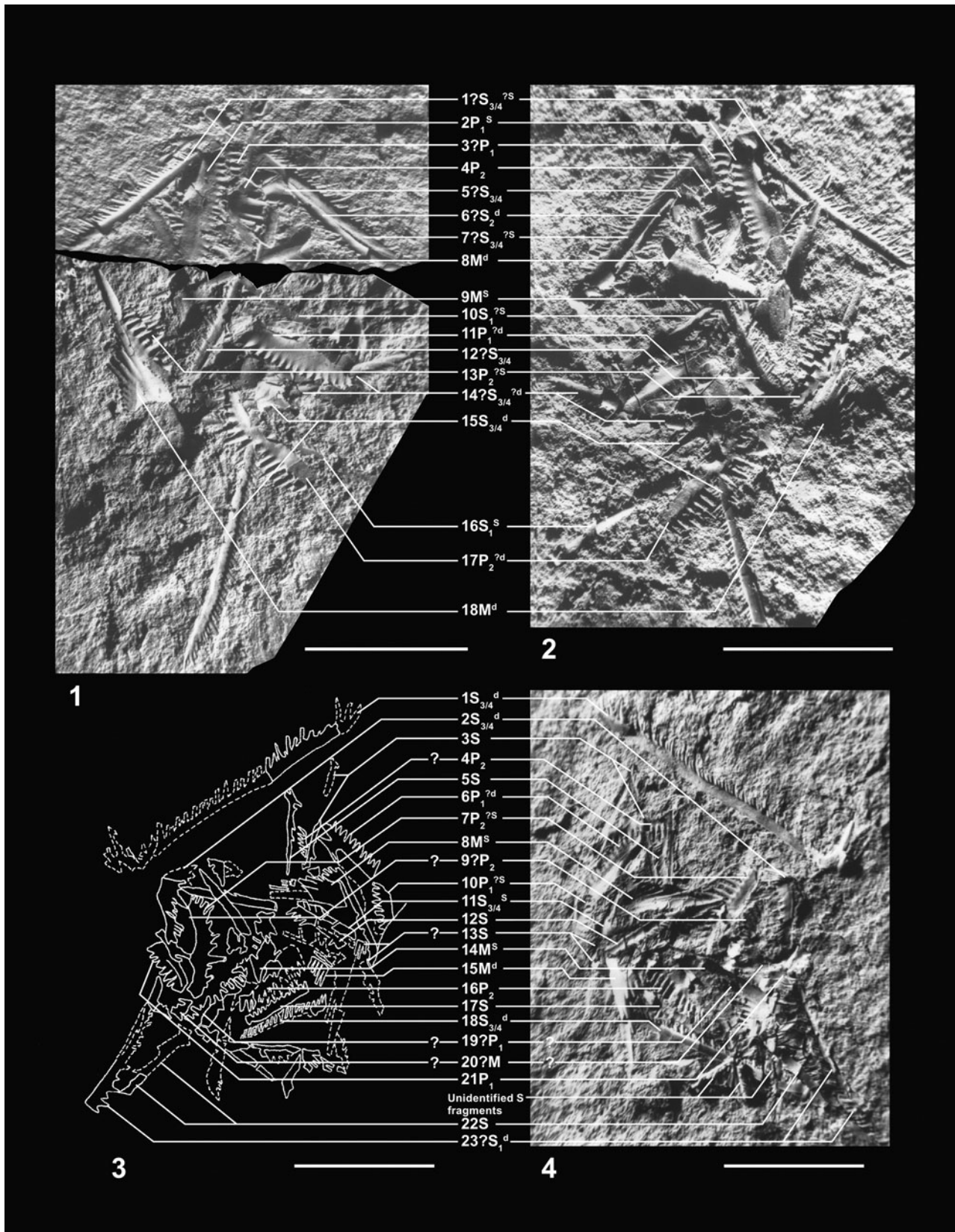


Figure 1. *Lochriea montanaensis* Scott, 1942, holotype and paratype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]). Scanning electron micrographs and outline drawing of bedding-plane assemblages on black shale, with interpretation of conodont elements present. Specimens reoriented relative to views shown by Scott (1942), and elements on parts and counterparts numbered sequentially from top down. Heath Formation, locality 2, Montana, USA. Scale bars = 0.5 mm. (1, 2) Fecal assemblage of 18 elements; holotype, part and counterpart (i.e., + and – of Scott [1942, pl. 37, figs. 2, 6], respectively), UI X-1318; (3, 4) fecal assemblage of 23 elements; paratype, part and counterpart (i.e., + and – of Scott [1942, pl. 37, figs. 4, 5]), respectively. Part (+) lost; outline drawing (3) based on Scott (1942, fig. 4), UI X-1319.

North America (Krumhardt et al., 1996), and in strata of equivalent age elsewhere in the world.

The earliest occurrences of a species of the genus are *Lochriea cracoviensis* (Belka, 1985), at the base of the Viséan in Poland (Belka, 1985, chart), and *L. cracoviensis* and *L. saharae* Nemyrovska, Perret-Mirouse, and Weyant, 2006, from the lower Viséan of Algeria (Nemyrovska et al., 2006), both species appearing slightly before *L. commutata* in the latter country. The upper limit of species of *Lochriea*, including that of *L. commutata*, is in the earliest Bashkirian (lowermost Morrowan) of Ukraine (Nemirovskaya et al., 1991), Uzbekistan (Nigmatganov and Nemirovskaya, 1992), south China (Wang et al., 1987b), southwest Japan (Mizuno, 1997), Spain (Sanz-López and Blanco-Ferrara, 2012), and the lower Namurian of Britain and Ireland (Higgins, 1985, table 7; Sweet, 1988, chart 6). The type species, *L. commutata*, is long ranging (Sweet, 1988, chart 6) and is of biostratigraphic utility only in a local context. *Lochriea commutata* and *L. homopunctatus* (Ziegler, 1960), were utilized by Metcalfe (1981) and Varker and Sevastopulo (1985) to define local-range zones. Other species, such as *L. cracoviensis*, *L. mononodosa* (Rhodes, Austin, and Druce, 1969), *L. nodosa* (Bischoff, 1957), *L. multinodosa* (Wirth, 1967), and others, have a more limited range and are therefore stratigraphically more useful (Higgins and Wagner-Gentis, 1982; Belka, 1985, chart; Sweet, 1988, chart 6). Atakul-Özdemir et al. (2012) suggested that *Lochriea homopunctatus* is globally important for marking and recognizing the base of the Viséan, and they indicated that the first appearance of *Lochriea zieglerei* Nemirovskaya, Perret, and Meischner, 1994, was under investigation as a marker for the Viséan/Serpukhovian boundary. Qi et al. (2018) provided occurrence data (fig. 2) for ten species of *Lochriea* at or near the Viséan/Serpukhovian boundary in south China; this data supports Sevastopulo and Barham (2014) and others in advocating for the use of the first appearance datum (FAD) of *L. zieglerei* as a definitive marker for the base of the Serpukhovian Stage. Qi et al. (2018, figs. 3, 4) also illustrated their interpretation of the evolutionary relationships among nine of the 10 *Lochriea* species recovered by them.

When Mizuno (1997) defined his new genus *Neolochriea*, he recognized four species, each of which was based solely on P₁ elements. He interpreted the four species of *Neolochriea* from Japan to be closely related to *Lochriea* spp., their morphology and stratigraphic distribution leading him to conclude that *Neolochriea* evolved from *Lochriea*. The first appearance of these *Neolochriea* species in southwest Japan is well within the Bashkirian (Morrowan), and it is above the occurrence of *L. commutata* in Japan and elsewhere in the world. In Japan, *L. commutata* ranges into the basal Bashkirian (i.e., into the *Declinognathodus noduliferous* Zone) (Mizuno, 1997). Although it is known to range higher into the basal Bashkirian of the Donets Basin of the Ukraine (Nemirovskaya et al., 1991) and south China (Wang et al., 1987b), the occurrence of *L. commutata* in Japan (Mizuno, 1997) is higher than has been recorded from Europe or North America.

Taxonomic journey of *Lochriea* Scott, 1942

Scott (1942, p. 298) defined the conodont genus *Lochriea* as “natural conodont assemblages made up of hindeodells,

spathognaths, prioniods, and prioniodells.” With the discovery by Melton and Scott (1973, p. 58) of what they believed to be complete conodont animals containing in situ elements in functional position, they amended this definition slightly to “conodont-bearing animals in which conodonts are represented by hindeodellids, spathognathodids, neoprioniodids, and prioniodinids-ozarkodinids.”

Most conodont researchers have worked, and continue to work, on discrete elements recovered by breaking down sedimentary rock with acids and solvents. However, the preceding definitions of the apparatus composition of *Lochriea* species were based entirely on the study of rare bedding-plane assemblages and, 30 years later in the early 1970s, on conodontophages with elements of *Lochriea* and other conodont genera in their gut. This created a dichotomy between the taxonomy of ornamented and unornamented P₁ conodont elements now accepted to be the P₁ elements of *Lochriea* spp., and the taxonomy based on bedding-plane assemblages. Thus, starting in 1941, the year before *Lochriea* was first named, and continuing into the 1990s, those workers studying these ornamented and unornamented P₁ elements generally assigned P₁ elements that have a morphology similar or identical to those present in these rare bedding-plane assemblages to a variety of genera. The earliest of these assignments was by Branson and Mehl (1941a, b), who assigned their new species *commutatus* to *Spathognathodus* Branson and Mehl, 1941 (Branson and Mehl, 1941b). A year later, Scott (1942)—working at a time when neither a procedure nor an agreement had been established for how to reconcile taxonomies based on discrete isolated conodonts with the very same ones found in bedding-plane assemblages—bypassed Branson and Mehl’s *Spathognathodus commutatus* in favor of his own *Lochriea montanaensis*.

Ironically, subsequent workers did their own bypassing of Scott’s conclusions regarding the bedding-plane assemblage-based *Lochriea* in favor of the better established, perhaps simpler, and (at the time) less controversial single-element taxonomy, thereby sending *Spathognathodus commutatus* and some other similar platform elements on a circuitous and complex taxonomic journey. Thus, Hass (1953, p. 80) assigned his new species *inornatus*, a junior subjective synonym of *commutatus*, to *Gnathodus* Pander, 1856, and recognized its similarity to *Gnathodus commutatus*, with Bischoff (1957, p. 22) apparently being the first to assign *Spathognathodus commutatus* to *Gnathodus*. This was followed by Ziegler in Flügel and Ziegler (1957, p. 39), Serre and Lys (1960, p. 39), Wirth (1967, p. 206), Rhodes et al. (1969, p. 95), Thompson and Goebel (1969, p. 23–24), Marks and Wensink (1970, p. 258), Aisenverg et al. (1979, p. 48), Metcalfe (1981), and Dong and Ji (1988, p. 50) also assigning *commutatus* to *Gnathodus*. Bischoff (1957), and others who followed, generally did not provide reasons for removing the species *commutatus* from *Spathognathodus*, although good reasons for doing so are that: (1) *Spathognathodus*, a replacement name for the previously occupied *Spathodus* Branson and Mehl, 1933, had become a catch-all genus used for a very broad range of bladed P₁ conodont elements in animals that evolved over long periods of geologic time; (2) *Lochriea commutata* P₁ elements are morphologically distinct from most spathognathodid P₁ elements by having a blade with more uniform denticulation and a subcircular posteriorly-positioned

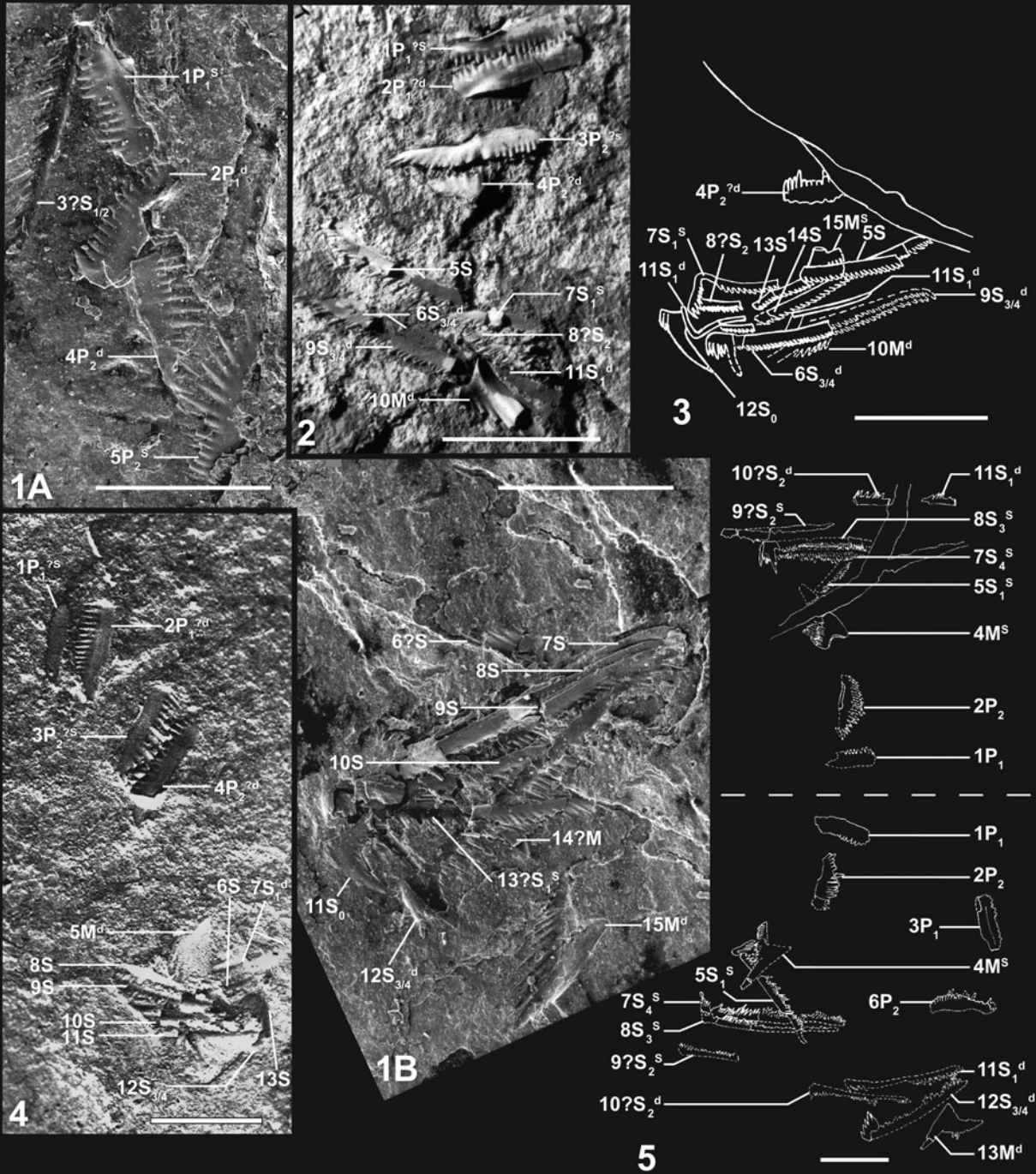


Figure 2. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b). Scanning electron micrographs (1A, 1B, 2), photomicrograph (4), and line drawings (3, 5) of bedding-plane assemblages on black shale surfaces. Solid lines (3, 5) represent elements and dashed lines, represent imprints of elements. Heath and Tyler formations, Montana, USA. Scale bars = 0.5 mm. (1A, 1B) Natural assemblage of 15 elements in lateral collapse with some rotation of P element complex, numbered diagonally from the upper left to lower right. Only part (i.e., of part and counterpart) is illustrated. Sample H-B-1-B, Tyler Formation, locality 3, ISGS 62P-207A. (2, 3) Natural assemblage of 15 elements in oblique lateral collapse pattern from the side (Purnell and Donoghue, 1998), numbered from the top down. Part and counterpart, respectively, with P₁ and P₂ element pairs in apposition mostly preserved on part (2), with anterior end of P₂rd element preserved on counterpart (3), which was drawn rather than photographed. More detail of S elements is shown on counterpart (3), although some M and S elements are only imprints. Sample H-B-1-B-1, Tyler Formation, locality 3, ISGS 62P-216A and 62P-216B. (4) Natural assemblage of 13 elements in oblique collapse from behind, above, and to one side (Purnell and Donoghue, 1998), numbered from the top down. P₁, P₂, and M^d elements are imprints. S element array is tightly clustered, preventing specific identification of six S elements present; anterior ends of elements 11S–13S further revealed by excavation subsequent to photo. Probable topotype, of which only part is known. Sample H-A-1-1, Heath Formation, locality 2, ISGS 62P-210. (5) Natural assemblage of 13 elements in apparent lateral collapse, but with disrupted architectural pattern, numbered consecutively from the mirror image axis (horizontal dashed line) outward; part (lower) and counterpart (upper) show some scatter. Sample H-A-2-7-1, Heath Formation, locality 2, ISGS 62P-218A and 62P-218B.

basal cavity; and (3) *Spathognathodus primus* Branson and Mehl, 1933, the type species of *Spathognathodus*, is a middle Silurian multielement conodont species, with its own complex nomenclatural evolution from *Spathognathodus primus* to *Hindeodella confluens* (Jeppsson, 1969, p. 15), to *Ozarkodina typica* (Klapper and Philip, 1971, p. 441, 443), to *O. confluens* (Klapper, 1973, p. 211, 221), and back to *O. typica* (see Murphy et al., 2004, for a revision of Silurian spathognathodids). Because the apparatus for *O. typica* is well known and restricted to the Silurian, neither *Spathognathodus* nor *Ozarkodina* can be used to accommodate the Carboniferous species *Lochriea commutata*.

Among the new conodont species and subspecies, based on P₁ elements with or without ornamentation that were being assigned to *Gnathodus*, were the subspecies *Gnathodus commutatus nodosus* Bischoff (1957, p. 23) and *G. commutatus multinodosus* Wirth (1967, p. 208), as well as the species *G. glaber* Wirth (1967, p. 210, 211) and *G. mononodosus* Rhodes et al. (1969, p. 103). However, by the late 1960s, some or all of these gnathodontids were increasingly understood to be morphologically and phylogenetically distinct from species with more complex ornamented P₁ elements, such as *G. bilineatus* (Roundy, 1926) and *G. girtyi* Hass, 1953. The result was the informal (Meischner, 1970), and then the formal (Higgins, 1975), naming of the genus *Paragnathodus* for some of these conodont species. *Paragnathodus* was first used as a nomen nudum by Meischner (1970, p. 1173, 1177, fig. 2); Higgins (1975, p. 70) subsequently defined the genus, with *Paragnathodus commutatus* as the type species, as follows: “The unit consists of a subrectangular blade and carina and a low, subcircular to subquadrate posterior cup. The oral surface of the blade is denticulate and is not clearly distinguished from the carina; the denticles of the blade increase in width posteriorly when seen in oral view. The aboral side of the cup is excavated.”

The genus *Lochriea* Scott, 1942, initially based on rare bedding-plane assemblages, was exhumed, in a sense by, Melton and Scott (1973) when they named conodontophages containing *Lochriea* sp. elements in their gut, *Lochriea wellsii*. Shortly thereafter, Norby (1976, p. 140) brought the genus into taxonomic play when, recognizing the priority of *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) over *Lochriea montanaensis* Scott, 1942, he applied this priority to designate *L. commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) the type species of *Lochriea*. That conclusion, and the resulting action, required a conciliation of concepts based on bedding-plane assemblages and discrete platform elements—one more than three decades in the making.

Norby’s work was not widely available and the generic designation *Paragnathodus* continued to be used, presumably by those who did not have access to, or who rejected Norby’s conclusions. Thus, Higgins (1981, p. 39, fig. 4.3, 4.6) continued his earlier practice (Higgins, 1975, p. 70) of placing *commutatus*, *nodosus*, *mononodosus*, and *cruciformis* in *Paragnathodus*, and adding *multinodosus* and *glaber*, the latter species apparently only in Higgins (1981, fig. 4.6). In that study, he recognized and defined a *Paragnathodus nodosus* conodont zone in the Brigantian (early Carboniferous) of Britain. In subsequent work, Higgins (1985, pl. 6.1, figs. 7, 8, 11, 12) also placed *commutatus* and *mononodosus* in *Paragnathodus*.

By 1982, Higgins (in Higgins and Wagner-Gentis, 1982) recognized the probable synonymy of *Paragnathodus* and *Lochriea* and commented (p. 335) that “the composition of the multi-element genus [*Paragnathodus*] is unknown but it is likely to correspond to the natural assemblage *Lochriea* of Scott 1942.” Higgins (1985, p. 214–215) subsequently assigned *commutata* and *mononodosa* to *Lochriea*; however, he continued to recognize *Paragnathodus* by placing *nodosus* in that genus while noting that Varker and Sevastopulo (1985) assigned that species to *Lochriea* (Higgins, 1985, p. 215, pl. 6.1, fig. 9 [caption under pl. 6.3, fig. 9]). In the same year, Grayson et al. (1985, p. 169) assigned *commutatus* from southern Oklahoma to *Paragnathodus*. Belka (1985, p. 40) recognized and described a new species of *Paragnathodus*, *P. cracoviensis*, and the next year von Bitter et al. (1986) referred “simple-cupped gnathodontiform” conodonts to that genus. Krumhardt et al. (1996) documented that Ji (1987), Riley et al. (1987), Wang et al. (1987a), Wang and Higgins (1989), Nemirovskaya et al. (1991), Varker et al. (1991), Nigmatganov and Nemirovskaya (1992), and Alekseev and Kononova (1993), among others, continued to assign *commutatus* to *Paragnathodus*, and we here add Yanagida et al. (1992) to that list.

Those authors who did have access to the unpublished work of Norby (1976), and agreed with his conclusion that *Lochriea* was the earliest valid generic designation available, began to use *Lochriea*, but without full documentation regarding why the name applies. Horowitz and Rexroad (1982, p. 966) may have been the first to do so when they reconstructed a partial apparatus of *L. commutata* from the Chesterian of the Illinois Basin based on statistical analysis, and when they attempted to extrapolate those results to *L. mononodosa* Rhodes, Austin, and Druce, 1969. By 1985, a number of authors had recognized either the utility, or the priority, of *Lochriea*. Varker and Sevastopulo (1985, p. 174, 181–183, pl. 5.5, figs. 11–13, 16–18, 20) referred

commutata, *nodosa*, and *mononodosa* to *Lochriea*, and applied each of the species names to a conodont zone. They also followed Rhodes et al. (1969, p. 160) and Marks and Wensink (1970, p. 266) in their designation of some M elements as *Neoprioniodus montanaensis*, and acknowledged (p. 202, pl. 5.6, fig. 13) that *Neoprioniodus singularis* (Hass, 1953), an M element, was “probably the Ne element of *Lochriea commutata*.”

Norby and Rexroad (1985) discussed similarities and associations of *Lochriea* with *Vogelgnathus*. And for the first time, Higgins (1985, p. 215, pls. 6.1, 6.3, and elsewhere) assigned *commutata* and *mononodosa* to *Lochriea* while, as noted earlier, continuing to place *nodosus* in *Paragnathodus* (Higgins, 1985, p. 215, pl. 6.3, fig. 9). The next year, Mapes and Rexroad (1986, p. 118) pointed out that the still widely used *Paragnathodus* was a junior synonym of *Lochriea*, an opinion subsequently shared by Stone (1991) and Skompski et al. (1995). Mapes and Rexroad (1986) described some elements of the *L. commutata* apparatus and noted the general agreement regarding the apparatus composition of the genus. Krumhardt et al. (1996) supported the use of *Lochriea* and documented the gradual acceptance of the genus by numerous workers since 1986, including Armstrong and Purnell (1987), Grayson (1990), Ramovš (1990a, b), Rexroad and Horowitz (1990), Whiteside and Grayson (1990), Weibel and Norby (1992), Kolar-Jurkóvsek and Jurkóvsek (1993), Nemirovskaya et al. (1994), and von Bitter and Norby (1994a, b). We add Purnell (1992) and Varker (1994) to this list, but make no claim that the citations before or after 1996 are either exhaustive or complete.

***Lochriea commutata*, parataxa, and a natural taxonomy governed by the International Code of Zoological Nomenclature**

Lochriea commutata (Branson and Mehl, 1941) (Branson and Mehl, 1941b), the type species of the genus, remains one of the most consistently recognized Carboniferous conodont species, despite its generic journey from *Spathognathodus* to *Gnathodus* to *Paragnathodus* to *Lochriea*. The principal aspect that prevented placement of *commutatus* in *Lochriea*, and indeed its recognition as the type species of *Lochriea* prior to Norby (1976), was that most Carboniferous conodont workers were working with discrete conodont elements rather than with the much rarer bedding-plane assemblages. A second reason is that the diagnoses of Scott (1942, p. 298) and of Melton and Scott (1973, p. 58) failed to recognize and acknowledge that elements present in bedding-plane assemblages, or in the gut of conodontophages (Conway Morris, 1985, 1990; Sweet, 1988, p. 28), had previously been identified and named. Specifically, although Scott (1942, p. 300) was probably aware of Branson and Mehl's (1941b) publication that included a description of *Spathognathodus commutatus*, he failed to recognize and acknowledge that the “spathognaths” present in *Lochriea* were both known and named. This resulted in the decades-long use of a dual nomenclature: one based on bedding-plane assemblages or similar uncommon material, and the other based on discrete elements.

Scott (1942, 1973) and Melton and Scott (1973), studying what they thought were whole taxa, were undoubtedly aware of earlier publications, but, in the thinking of the times, they bypassed the priority of previously named discrete conodonts.

Considerable debate had arisen before (e.g., Croneis, 1939) and after (e.g., Moore, 1962), but little agreement was found in how to deal taxonomically with fragmentary versus whole fossil material. One of the proposed solutions was to create and use parataxa (i.e., to maintain a parallel but taxonomically separate classification system independent of the International Code of Zoological Nomenclature [ICZN]) for fragmentary fossils such as crinoid ossicles, holothuroid spicules, fish remains, and conodonts. With conodonts the problem was twofold. The first was how to name discrete, individual elements, whether that was according to their shape, denticulation, or other criteria. And second, after conodont bedding-plane assemblages were discovered and named first by Hinde (1879), and subsequently by Scott (1934) and Schmidt (1934b), the question arose of whether the names of previously named discrete conodonts should have nomenclatural priority, when several different kinds of already named conodont elements were present in bedding-plane assemblages. Scott (1942) and fellow conodont workers before and after him were undoubtedly aware of this dilemma and gave it much thought; however, being unable to untie this particular taxonomic Gordian knot, they bypassed previously named taxa based on discrete conodont elements and created new taxonomic categories based on bedding-plane assemblages. Thus, Scott (1942) named *Lewistownella* for bedding-plane assemblages that contained the earlier-named diagnostic platform element *Cavusgnathus* Harris and Hollingsworth, 1933, also bypassing the earlier-named species *Spathognathodus commutatus* when he named *Lochriea montanaensis*. As late as a decade later, Rhodes (1953) named *Scottognathus* on the basis of bedding-plane assemblages from the Pennsylvanian of Illinois, bypassing the Law of Priority set by the ICZN, even though Gunnell (1931) and Stauffer and Plummer (1932) had previously named the diagnostic platform elements present in these assemblages *Idiognathodus* and *Streptognathodus*, respectively. Much the same situation prevailed with the recognition and naming of *Illinella* and *Duboisella* based on bedding-plane assemblages, while avoiding the available and earlier-named *Gondolella* Stauffer and Plummer, 1932 and *Idiopriodontus* Gunnell, 1933, respectively (Rhodes, 1952).

Conodont workers and other paleontologists of the time continued to wrestle with the paleontological angst created by the question of how to deal taxonomically with isolated fragmentary fossil remains. One result was the proposal to the ICZN by Moore and Sylvester Bradley (1957a, p. 5) for the recognition and use of parataxa “as a special category for the classification and nomenclature of discrete fragments or of life-stages of animals which are inadequate for identification of whole-animal taxa, with proposals of procedure for the nomenclature of Parataxa” (see Moore and Sylvester Bradley, 1957b, regarding the application of parataxa to conodonts). Rhodes (1962, p. W82) described the rather hasty rejection of this proposal by the ICZN in 1958, noting that the body “offered no alternative solution” and that “this action leaves conodont nomenclature in a confused and unstable position.” In discussing the taxonomic problems of a dual nomenclature, Rhodes (1962, p. W81) favored giving “new names to natural conodont assemblages and to retain the existing system of nomenclature for isolated conodonts.” Moore (1962, p. W92–W97) discussed the illegality of a dual classification and suggested adopting a

conservative course such that “species, genera and families distinguished on the basis of discrete conodonts . . . are to be regarded as “natural” taxa, and the species and genera defined on the basis of conodont assemblages likewise.”

The summary refusal of the ICZN may, however, have had the beneficial effect of forcing conodont workers to try harder to reconstruct apparatuses from collections of discrete conodont elements, and to name them according to the priority of the most characteristic named element, generally, but not always, the P₁ element. Simultaneous with the debates for and against the use and legality of parataxa, the stirrings of a revolution in conodont taxonomy were taking place in Germany. Here, Tatge (1956) and Huckriede (1958), studying Triassic conodonts, and Walliser (1964), working on Silurian conodonts, grouped discrete conodonts into tentative apparatuses, but without formally naming them.

By the mid-1960s, American Ordovician conodont workers Webers (1966) and Bergström and Sweet (1966) not only reconstructed apparatuses from discrete conodont collections, but also named them in conformity with the ICZN Law of Priority. Clearly, the revolution in conodont taxonomy was taking hold, and at the 1971 Symposium on Conodont Taxonomy, the Marburg Proposal (Aldridge and von Bitter, 2009, appendix II), with F.H.T. Rhodes as its prime mover, and its strong emphasis on strict application of the ICZN Code, passed with no further mention of parataxa. Some of the younger Carboniferous conodont workers who participated in the Marburg Symposium, or whose better-financed PhD advisors were there to later pass the ideas and recommendations of that meeting on to their students, correctly read the taxonomic winds that were blowing in conodont taxonomy. They did this by taking up the challenges of multielement taxonomy, and in quick succession (von Bitter, 1972; Baesemann, 1973; Perlmutter, 1975; Norby, 1976) began to reconstruct conodont apparatuses, and gave priority to the earliest validly named genus name, such as *Streptognathodus*, *Idiognathodus*, *Cavusgnathus*, and *Gondolella*, irrespective of how whole or fragmentary the original material used to describe these genera had been. Subsequent to 1971, even though students of some other fossil groups decided to continue to use parataxa, conodont workers overwhelmingly distanced themselves from parataxa and agreed to use a natural taxonomy governed by the International Code of Zoological Nomenclature. This group decision by members of the Pander Society was subsequently recognized by the ICZN (Melville, 1981).

Among bedding-plane assemblage-based generic names, such as *Scottognathus*, *Duboisella*, and *Illinella*, practically none are now used or invoked by Carboniferous conodont workers. All three are junior synonyms of earlier named taxa and are now mostly of historical interest. *Lochriea*, however, is the exception and survives because, unlike these three named bedding-plane assemblages, no previously assigned competing Carboniferous generic name based on discrete element taxonomy was, and is, available.

Taxonomic notes

We conclude, as did Norby (1976), that *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) is the senior subjective synonym of *Lochriea montanaensis*

Scott, 1942 and that the two are combined as *L. commutata* according to priority and availability. First and foremost, that conclusion is based on our detailed comparison and documentation (von Bitter and Norby, 1994a; Fig. 3) of the overall morphology of P₁ elements in the type specimens of *L. montanaensis* Scott, 1942 with the P₁ elements that are the type specimens of *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) (von Bitter and Norby, 1994a; Fig. 3), and of a wide range of P₁ elements from across North America and Europe (von Bitter and Norby, 1994a; Fig. 3). Our determination, based on this wide-ranging material, is that no apparent differences exist in overall P₁ morphology of the two taxa. Although the P₁ elements of the type specimens of *Lochriea montanaensis* tend to be longer than those of *L. commutata*, this observation has yet to be confirmed statistically. Discrete P₁ elements from the Heath Formation and from the overlying Tyler Formation of Montana, show considerable variation in morphological features such as the length and number of denticles, variation that we regard as normal phenotypic variation; however, further study may determine that this variation is ecophenotypic, and may be due to environmental differences during the deposition of the Heath and Tyler formations.

Second, our conclusion is based on our earlier determination (von Bitter and Norby, 1994b) that the well-developed microsculpture on the carinal denticles of P₁ elements of the type specimens of *Lochriea montanaensis* Scott, 1942, is not a defining characteristic of that taxon. Although this feature is obscured by diagenetic overgrowths on the lectotype and the paralectotypes of *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) (von Bitter and Norby, 1994a), that feature is present and was documented in the same study on more recently collected topotypes of *S. commutatus*. Additionally, P₁ elements of this morphology from a wide range of locations, including those from the Heath and Tyler formations of Montana, the Fayetteville Formation of Oklahoma, and the Herdringen Formation of Germany, exhibit this microsculpture (von Bitter and Norby, 1994a, b).

The weight of evidence supporting our conclusion that *Lochriea montanaensis* Scott, 1942 is a subjective junior synonym of *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b), was based initially (von Bitter and Norby, 1994a) on our comparison of the characteristics, particularly the micromorphology, of their P₁ elements. Conodont P₁ elements had long been regarded as the most diagnostic and most quickly evolving elements, and *S. commutatus* was, when described and named by Branson and Mehl (1941b), based solely on P₁ elements. We (von Bitter and Norby, 1994a) determined that the macro- and micromorphology of the P₁ elements of the two species were identical, concluding that they were synonyms of each other, and with the genus name *Lochriea* and the species name *commutatus* each having priority, that its correct name was, after amending the species name ending, *Lochriea commutata*. We here extend our documentation of *L. commutata* P₁ elements by illustrating specimens from the United States, Canada, and Germany (Fig. 3), and re-illustrating the lectotype of *Spathognathodus commutatus* from its type stratum and type locality, the Hindsville Formation of Oklahoma at locality 4 (Fig. 3.7–3.10). We had

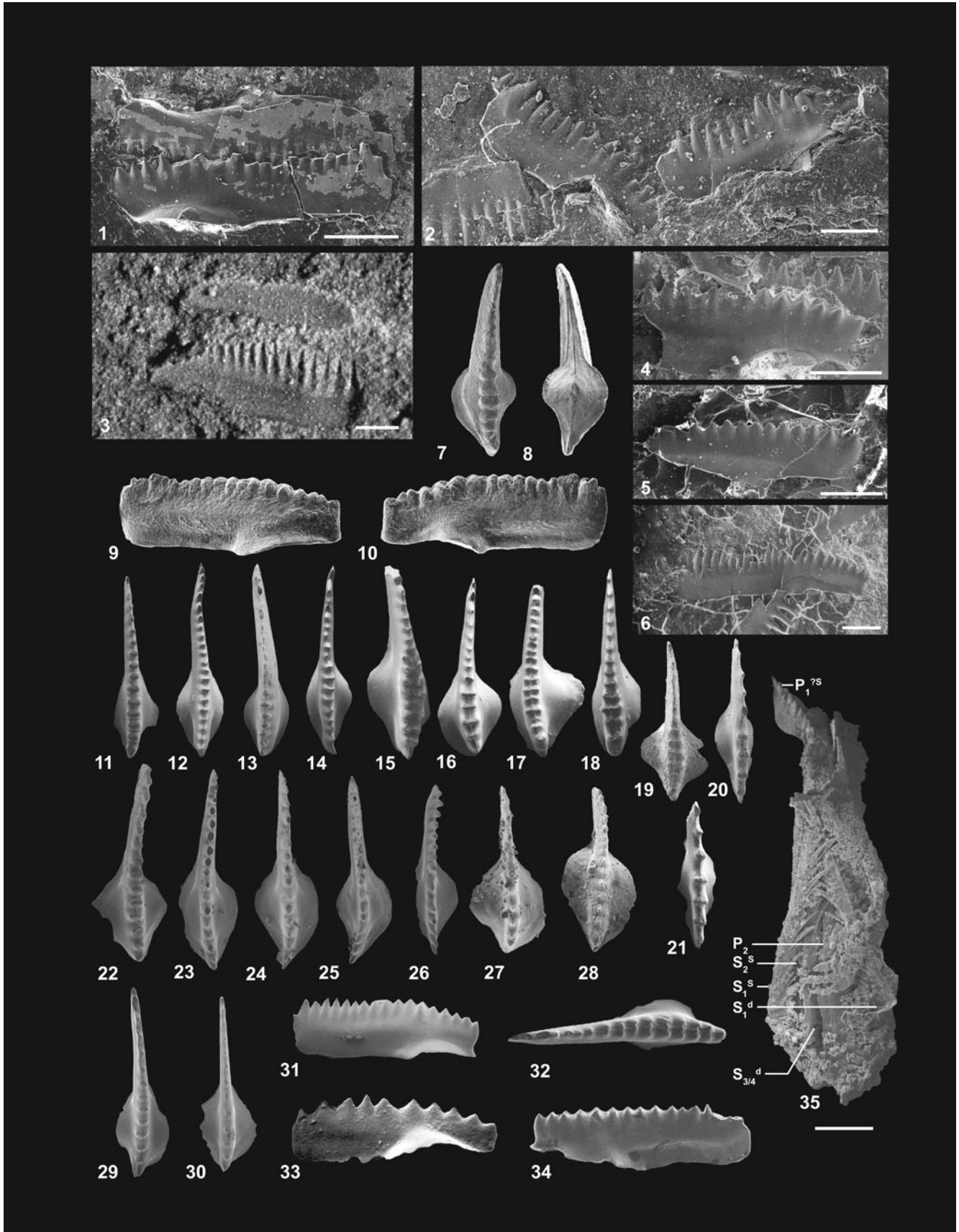


Figure 3. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) P₁ elements in bedding-plane assemblages on black shale (1–6), as acid residue-derived discrete elements (7–34), and in acid residue-derived fused assemblages (35). All are scanning electron micrographs except (3), which is a photomicrograph. Scale bars (1–6, 35) = 0.2 mm; for the remaining figures, actual specimen lengths are provided in descriptions below. (1) P₁^{s,d} element pair in functional apposition, lateral view along rostrocaudal axis of apparatus; element pair rotated ~90° from original functional position in apparatus. Anterior ends of elements on right side of figure, posterior on left. See elements 1P₁^{7s} and 2P₁^{7d} (Fig. 2.2) for apparatus context of P₁^{s,d} element pair. Spotty mottled surface attributable to uneven scanning electron micrograph coating, charging, or both. Sample H-B-1-B-1, Tyler Formation, locality 3, Montana, USA, ISGS 62P-216A. (2) P₁^{s,d} element pair in ‘near’ functional position in lateral view along rostrocaudal axis of apparatus with anterior ends of elements on right, posterior ends on left. P₁^s element both ‘flipped’ and rotated ~135° relative to its original functional apposition with P₁^d element. See elements 1P₁^s and 2P₁^d (Fig. 2.1A) for apparatus context of this element pair, and see element 4P₂^d (Fig. 2.1A) for apparatus context of anterior part of the P₂^d element on bottom left. Sample H-B-1-B, Tyler Formation, locality 3, Montana, USA, ISGS 62P-207A. (3) P₁^{s,d} element imprint pair in ‘near’ functional position, lateral view along rostrocaudal axis of apparatus, P₁^{7s} (upper) element rotated 180° relative to its original functional apposition with P₁^{7d} (lower) element. P₁^{7d} element a good imprint, P₁^{7s} element a partial imprint only. See elements 1P₁^{7s} and 2P₁^{7d} (Fig. 2.4) for apparatus context of the P₁^{s,d} element pair. Sample H-A-1-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-210. (4) P₁^s element (in) *Lochriea montanaensis* Scott, 1942 holotype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]), outer view. See element 2P₁^s (Fig. 1.1, 1.2) for apparatus context. Previously illustrated by von Bitter and Norby (1994a, fig. 2.1, counterpart). Heath Formation, locality 2, Montana, USA, UI X-1318. (5) P₁^{7d} element (in) *Lochriea montanaensis* Scott, 1942 holotype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]), outer view. See element 11P₁^{7d} (Fig. 1.1, 1.2) for apparatus context. Previously illustrated by von Bitter and Norby (1994a, fig. 2.2). Heath Formation, locality 2, Montana, USA, UI X-1318. (6) P₁^{7d} element, (?) inner view. Heath Formation, locality 1, Montana, USA, CM 33965. (7–10) P₁^s element, upper, lower, outer, and inner views, respectively, of a syntype of *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b). Designated as one of four cotypes and illustrated (with incorrect number UM C552-1) by Lane and Straka (1974, figs. 40.15, 40.16); catalogue no. UM C552-2 apparently applied by or at UM for series of four syntypes. Re-illustrated and designated lectotype (UM C552-2) of the species (other three specimens designated as paralectotypes and given new numbers) by von Bitter and Norby (1994a, figs. 2.6–2.9). Hindsville Formation, locality 4, Oklahoma, USA. Length = 0.91 mm. (11–18) P₁^s elements (14, 16–18) and P₁^d elements (11, 12, 13, 15), upper views of approximate ontogenetic growth series from least to most mature. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1088 to 62P-1092, and 62P-1094 to 62P-1096. Lengths = 0.63, 0.89, 1.00, 0.82, 0.78, 0.62, 0.68, and 0.63 mm, respectively. (19–21) P₁^d (19), P₁^{7d} (20), P₁^{7d} (21) elements, upper views of three elements from most to least mature. Samples VS-1, VS-12, and VS-12, respectively, Ridenhower Formation, locality 7, Illinois, USA, ISGS 62P-1201, 62P-1202, and 62P-1093. Lengths = 0.55, 0.47, and 0.43 mm, respectively. (22–27) P₁^s (22, 23, 26) and P₁^d (24, 25, 27) elements, upper views of a potential ontogenetic growth series from most to least mature. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593924–593928 and 696950. Lengths = 0.61, 0.60, 0.55, 0.62, 0.61, and 0.43 mm, respectively. (28) P₁^d element, upper view. Sample Kenk-2-1, Kennetcook Member, Upper Windsor Group, locality 9, Colchester County, Nova Scotia, Canada, ROM 63699. Length = 0.75 mm. (29, 30) P₁^d elements, upper views. Sample Schälk 42, Herdringen Formation, locality 10, North-Rhine Westphalia, Germany, ISGS 82P-53 and ISGS 82P-54, respectively. Lengths = 0.54 and 0.37 mm, respectively. (31) P₁^d element, inner view. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1101. Length = 0.79 mm. (32, 34) P₁^d element, upper and inner (caudal) views, respectively. Illustrated by Lane and Straka (1974, fig. 37.1, 37.2), Goddard Formation, locality 6, Oklahoma, USA, SUI 33624. Length = 0.94 mm. (33) P₁^{7d} element, (?) inner view of immature element, Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1097. Length = 0.44 mm. (35) P₁^{7s} element in ? upper view at posterior end of partial, fused S element array (see Fig. 9.21 for another view of this fused cluster). Apparatus showing several S elements of apparatus inclined toward one another. Collection USGS 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593966.

previously illustrated both its lectotype and its three paralectotypes (von Bitter and Norby, 1994a, figs. 2.6–2.15, 3.1–3.12), as well as P₁ elements from the overlying Fayetteville Formation at locality 5 (Sutherland and Manger, 1979, fig. 2 correlation chart) (von Bitter and Norby, 1994a, fig. 5.1–5.12).

Because *L. montanaensis* Scott, 1942, was based on bedding-plane assemblages that contained elements other than P₁ elements, the key to confirming our earlier conclusion that *L. montanaensis* and *S. commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) were synonyms of one another, lay in demonstrating that their non-P₁ elements (i.e., their P₂, M, S₀, S₁, S₂, and S_{3/4} elements) were also identical. Thus, we re-collected the type locality and type stratum of *S. commutatus*, the Hindsville Formation at locality 4 in Oklahoma, from which we recovered a few P₂, M, S₀, and S_{3/4} elements that we identified as belonging to that species, as well as more than a dozen toptotype P₁ elements, and compared the non-P₁ elements from there with the homologous elements in the type specimens of *Lochriea montanaensis* Scott, 1942 (Scott, 1942, pl. 37, figs. 2, 4–6; here re-illustrated in Fig. 1). We continued this process of comparing and documenting non-P₁ elements with those homologous elements in toptotype specimens of that species collected by Norby (1976) from the Heath Formation, at locality 2, in Montana (Fig. 2). Finally, we examined and documented P₂, M, S₀, S₁, S₂, and S_{3/4} elements, which we here identify and label as those of *L. commutata*, from a variety of localities in the United States, Canada, and Germany (Figs. 4–9). One of these localities, the Fayetteville Formation at locality 5 in Oklahoma (Sutherland and Manger, 1979, fig. 2), yielded characteristic and slightly better-preserved *L. commutata* P₂, M, S₀, and S_{3/4} elements (Figs. 5.15, 6.12, 9.17, 9.18) than the non-P₁ elements we recovered from the Hindsville Formation at locality

4. We conclude, after examining and comparing lower Carboniferous conodont faunas from three countries on two continents, that the P₂, M, S₀, S₁, S₂, and S_{3/4} elements, like the P₁ elements of the initially designated *S. commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b), the subsequently named *L. montanaensis* Scott, 1942, and those of the final combination, *L. commutata*, show surprisingly little variation within each of the non-P₁ elements, confirming that *L. montanaensis* and *L. commutata* are indeed synonyms.

Previously, we (von Bitter and Norby, 1994a, b) regarded Branson and Mehl (1941b) as having provided the taxonomic foundation for the species *Spathognathodus commutatus* Branson and Mehl. We still do so, despite subsequently having become aware that E.B. Branson and M.G. Mehl had published an article a few months earlier (Branson and Mehl, 1941a) in which they used the name *S. commutatus* for illustrated specimens from the Caney Formation of Oklahoma, but without having fulfilled the requirements for naming a new species. In effect, the authors were using a nomen nudum, a condition they rectified a few months later in Branson and Mehl (1941b) when they described, named, and illustrated the species more adequately from material from the ‘Pitkin limestone’ (now Hindsville Formation) of Oklahoma.

In addition to describing *Lochriea montanaensis*, Scott (1942, p. 299) also described a second species of the genus, *L. bigsnowyensis*. This description was also based on bedding-plane assemblages from the Heath Formation of Montana, the one specimen (the holotype) still available, being composed of a complement of 14 elements (Fig. 10). However, unlike *L. commutata*, it cannot contribute either to the generic concept of *Lochriea* or to our knowledge of the apparatus composition and structure of its species. Scott (1942, p. 299) described the

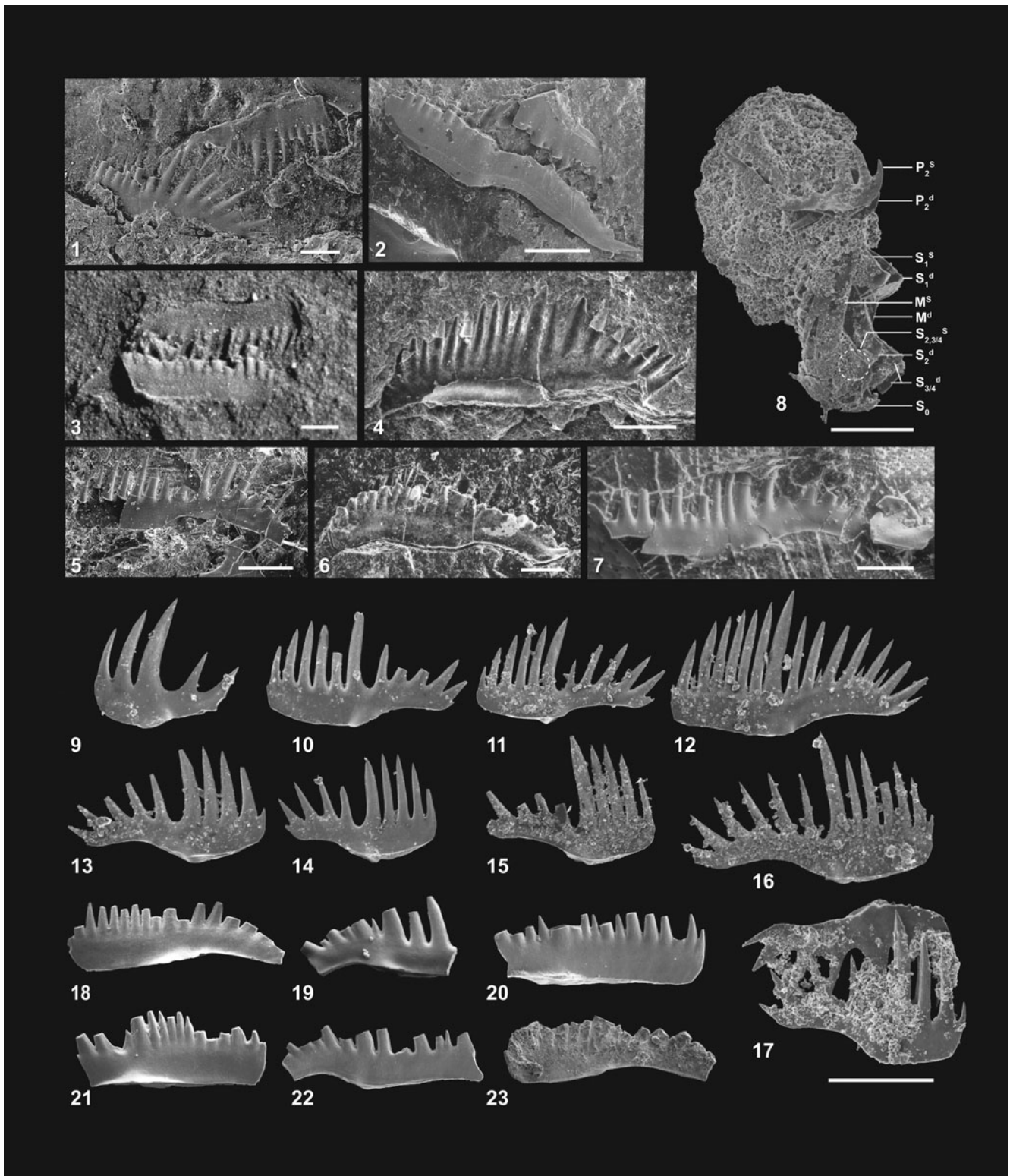


Figure 4. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) P₂ elements in bedding-plane assemblages on black shale surfaces (1–7), in acid residue-derived fused assemblages (8, 17), and as acid residue-derived discrete elements (9–16, 18–23). All are scanning electron micrographs except (3), which is a photomicrograph. Scale bars (1–8, 17) = 0.2 mm. For the remaining figures, actual specimen lengths are provided in descriptions below. (1) P₂^{s,d} element pair in lateral view along rostrocaudal axis of apparatus, (upper) P₂^d element rotated ~135° relative to (lower) P₂^s element ‘in apposition’ position. See elements 4P₂^d and 5P₂^s (Fig. 2.1A) for apparatus context of P₂^{s,d} element pair. Sample H-B-1-B, Tyler Formation, locality 3, Montana, USA, ISGS 62P-207A. (2) P₂^{s,d} element pair view along rostrocaudal axis of apparatus. Anterior part of P₂^d element missing, but preserved on counterpart ISGS 62P-216B (Fig. 2.3). See elements 3P₂^s and 4P₂^d (Fig. 2.2, 2.3) for apparatus context of P₂^{s,d} element pair (however, P₂^{s,d} elements as shown in Fig. 2.2 are reversed relative to the position shown here). Sample H-B-1-B-1, Tyler Formation, locality 3, Montana, USA, ISGS 62P-216A. (3) P₂^{s,d} element pair in apposition in lateral view along rostrocaudal axis of apparatus. Lower P₂^d element is imprint only. See elements 3P₂^s and 4P₂^d (Fig. 2.4) for apparatus context of P₂^{s,d} element pair. Sample H-A-1-1, locality 2, Heath Formation, Montana, USA, ISGS 62P-210. (4) P₂ element as (mostly) impression in ‘inner view’; only a few denticle tips of element preserved; posterior termination not preserved. See element 2P₂ (Fig. 2.5) for apparatus context. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218B. (5) P₂^{7d} element (in *Lochriea montanaensis* Scott, 1942 holotype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]) in ‘inner view’. See element 17P₂^{7d} (Fig. 1.1, 1.2) for apparatus context of this element. Heath Formation, locality 2, Montana, USA, UI X-1318. (6) P₂ element in ‘inner view’, posterior tip broken and not present. See element 6P₂ (lower Fig. 2.5) for apparatus context. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218A. (7) P₂^{7d} element, ‘inner view’. Heath Formation, locality 1, Montana, USA, CM 33965. (8) P₂^{s,d} element pair in approximate functional apposition in lateral view along rostrocaudal axis of nearly complete sinistral side of a fused apparatus (see Figs. 5.4, 7.7 for other views of this element pair in this apparatus). USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM-593967. (9–16) P₂ elements, ?outer lateral views of two ontogenetic growth series (9–12) and (13–16) from smallest to largest. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593929–593936. Lengths = 0.28, 0.54, 0.60, 0.70, 0.45, 0.45, 0.53, and 0.55 mm, respectively. (17) P₂^{s,d} element pair fused in functional apposition, lateral view. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593968. (18) P₂^d element, inner view. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1102. Length = 0.50 mm. (19–22) P₂^s elements, inner views. Samples VS-12, VS-5, VS-1, and VS-5, Ridenhower Formation, locality 7, Illinois, USA, ISGS 62P-1117, 62P-1205, 62P-1116, and 62P-1206. Lengths = 0.47, 0.52, 0.44, and 0.61 mm, respectively. (23) P₂^d element, inner view. Sample HerbR-7-7, Herbert River Limestone, Upper Windsor Group, locality 9, Nova Scotia, Canada, ROM 63700. Length = 0.73 mm.

defining P₁ elements (= his spathognaths) of *L. bigsnowyensis* as “blade wide, thin along aboral margin; denticles short, tips rounded, escutcheon moderately deep” adding (p. 299) that “only imprints and fragments of spathognaths have been found in assemblages of *L. bigsnowyensis*. As a result no sharp differences can be pointed out at this time.” Presumably, the “sharp differences” he alluded to referred to differences between the P₁ elements of this and related species, such as *L. commutata*.

Scanning electron microscopy of the bedding-plane assemblage designated by Scott (1942) as the holotype of *L. bigsnowyensis* demonstrates (Fig. 10) that it contains one or more carminiscaphate P₁ elements, as well as P₂, M and S elements (Fig. 10) similar or identical to those present in apparatuses of *Cavusgnathus* spp. (von Bitter and Merrill, 1990, fig. 1B–D; Purnell and Donohue, 1998, text-fig. 15). The bedding-plane assemblage Scott (1942, p. 299) designated as the paratype, but did not illustrate, has been lost. We place the discrete *L. bigsnowyensis* prioniod element of Scott (1942, pl. 40, fig. 3) in synonymy with the *L. commutata* M element. The prioniodell elements illustrated by Scott (1942, pl. 40, figs. 4 and 5) may be *L. commutata* P₂ elements.

We conclude that *L. bigsnowyensis* was based primarily on a partial bedding-plane assemblage of an as yet unidentified species of *Lewistownella* Scott, 1942, which in turn is a junior synonym of an as yet unidentified species of *Cavusgnathus* Harris and Hollingsworth, 1933. *Lochriea bigsnowyensis* was also, but to a minor degree, based on a misidentified discrete M element that we place in *L. commutata* and on two P₂ elements that may have belonged to *L. commutata*.

Element composition of the *Lochriea commutata* apparatus

Scott (1942, p. 298, fig. 1) concluded that the *Lochriea montanaensis* apparatus bore a minimum of 22 elements, comprising at least four each of “spathognaths,” “prioniodells,” and “prioniods,” and at least ten “hindeodells” (Fig. 11.1, 11.2), an element terminology that translates into four each of carminiscaphate,

angulate, and makellate elements, as well as ten bipennate elements, respectively (Fig. 11.1, 11.2).

Thirty-one years later, Melton and Scott (1973) named newly discovered fossils of a soft-bodied, cigar-shaped animal, *Lochriea wellsii*, because of conodont elements they recognized as those of a species of *Lochriea*, in the “deltaenteron,” or midgut, of the animal. Melton and Scott (1973) referred to these elements as “spathognathodids,” “prioniodinids/ozarkodinids,” “neoprioniodids,” and “hindeodellids” (Fig. 11.2). Scott (1973) in discussing this species, identified the “spathognathodids” as “a platform type” and suggested a possible ratio of the four element types present as 3:1:3:10 (Fig. 11.2), but admitted that the exact number of each was questionable. The species was subsequently assigned to a new genus by Conway Morris (1985), and was interpreted, as *Typhloesus wellsii* (Melton and Scott), to be a conodontophage (i.e., a conodont-eater) (Conway Morris, 1985, 1990), an interpretation supported by Sweet (1988) and by us. Reasons for our support for this conclusion are that: (1) elements of other conodont taxa, including those of *Kladognathus* Rexroad, 1958, have been found inside *T. wellsii* (Conway Morris, 1990; Purnell, 1993a); (2) elements of *Lochriea* observed and reported in *T. wellsii* are disorganized and jumbled; and (3) there is, notwithstanding the orderliness of the *Kladognathus* assemblage described by Purnell (1993a), a general uncertainty and inconsistency regarding the number and identity of *Lochriea* elements in *T. wellsii*. We conclude that the identity and apparatus composition of the species of *Lochriea* present in the gut of *T. wellsii* has yet to be determined and is presently of no help in elucidating the apparatus structure of *L. commutata*, or that of the genus *Lochriea*.

Scott (1942, p. 293) wrote that the bedding-plane assemblages he was studying “did not represent accidental accumulations or coprolite material.” Nevertheless, most of the elements in his illustrated bedding-plane assemblages show a definite lack of orientation and are best described as chaotic. The single exception (Scott, 1942, pl. 38, fig. 10; vide UI X-1385) is a symmetrical bundle of eight “hindeodells” (= S elements) with “four oriented with the denticles to the left and four to the right,” that he identified (p. 295) as *L. montanaensis*. This partial S-element

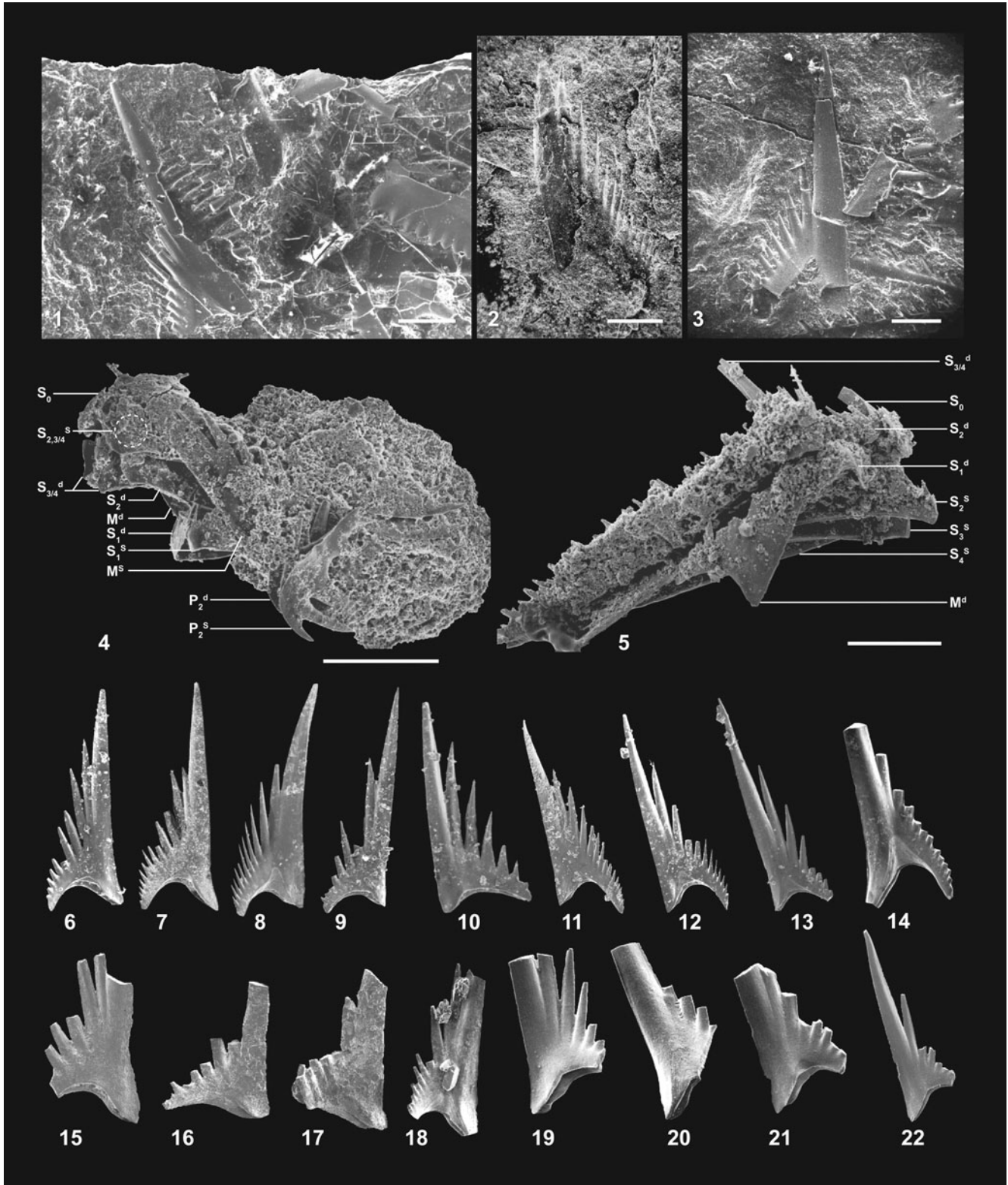


Figure 5. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) M elements in bedding-plane assemblages (1–3), in acid residue-derived fused assemblages (4, 5), and as acid residue-derived discrete elements (6–22). Scale bars (1–5) = 0.2 mm. For the remaining specimens, actual lengths from cusp tip to anticusp are provided in descriptions below. (1) M^d element in *Lochriea montanaensis* Scott, 1942 holotype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]) in outer (dorsal) view. See element 18M^d (Fig. 1.1, 1.2) for apparatus context. Heath Formation, locality 2, Montana, USA, UI X-1318. (2) M^d element imprint in outer view. See element 15M^d (Fig. 2.1B) for apparatus context. Sample H-B-1-B, Tyler Formation, locality 3, Montana, USA, ISGS 62P-207A. (3) M^e element in inner view, Heath Formation, locality 1, Montana, USA, CM 33965. (4) M^{s,d} elements in outer view of sinistral side of moderately complete apparatus (see Figs. 4.8, 7.7 for other views of this apparatus and element pair). USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593967. (5) M^d element in outer view of moderately complete S–M element array (see Fig. 6.6, 6.7 for other views of this apparatus). USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593969. (6–9) M^s elements, inner views of well-preserved ontogenetic growth series. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593937–593940. Cusp tip to anticusp = 0.69, 0.85, 0.81, and 0.57 mm, respectively. (10–13) M^d elements, inner views of well-preserved ontogenetic growth series. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593941–593944. Cusp tip to anticusp = 0.49, 0.84, 0.76, and 0.76 mm, respectively. (14) M^d element, inner view. Sample Schälk 50, Herdringen Formation, locality 10, North-Rhine Westphalia, Germany, ISGS 82P-45. Cusp tip to anticusp = 0.43 mm. (15) M^s element, inner view. Sample 2, Fayetteville Formation, locality 5, Craig Co., Oklahoma, USA, ISGS 82P-46. Cusp tip to anticusp = 0.23 mm. (16, 17) M^s elements, inner views, showing crystal overgrowths and surface etching. Sample Kenk-2-1, Kennetcook Member, Upper Windsor Group, locality 9, Colchester Co., Nova Scotia, Canada, ROM 63701 and 63702, respectively. Cusp tip to anticusp = 0.44 and 0.49 mm, respectively. (18) M^s element, inner view. Sample Schälk 50, Herdringen Formation, locality 10, North-Rhine Westphalia, Germany, ISGS 82P-47. Cusp tip to anticusp = 0.82 mm. (19, 20) M^d elements, inner views. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1112 and 62P-1113, respectively. Cusp tip to anticusp = 0.43 and 0.65 mm, respectively. (21, 22) M^d elements, inner view. Samples VS-12 and VS-7, Ridenhower Formation, locality 7, Illinois, USA, ISGS 62P-1111 and 62P-1207, respectively. Cusp tip to anticusp = 0.37 and 0.84 mm, respectively.

assemblage may have been the one of the important clues, along with the presence of sinistral and dextral elements, that Scott (1942, fig. 1) used to arrive at his schematic diagram (Fig. 11.1) (although he did not specifically state that his assemblages represented bilaterally symmetrical apparatuses within the conodont animal, his diagram certainly implies that). Norby (1976) described Scott's apparatuses of *Lochriea* as having "a scattered arrangement," and he regarded all but this single specimen as fecal. Proof that Scott's *Lochriea* assemblages were indeed fecal was provided by the numerous additional assemblages of *L. commutata* collected by Norby (1976) and the single bedding-plane assemblage collected by R. Lund in the Heath Formation of Montana, Scott's original collecting unit, as well those found by Norby (1976) in the overlying Tyler Formation. The best of Norby's bedding-plane assemblages are natural assemblages in which the elements show good parallel arrangement and pairing (Fig. 2).

Figure 12 illustrates a two-dimensional exploded diagrammatic view of the relative position and arrangement of elements in the three-dimensional functional feeding apparatus of *L. commutata*. Aldridge et al. (1987) and Purnell and Donoghue (1997, 1998, text-fig. 1) proposed and reviewed possible three-dimensional arrangements of elements within the functioning ozarkodinid conodont apparatus, with Purnell and Donoghue (1998) concluding that their text-figure 1E best explained the position, arrangement, and functional morphology of elements in that apparatus.

Scott (1942, p. 299) recognized that the *Lochriea montanaensis* apparatus contained "at least ten hindeodells" (Fig. 11). This bundle of mostly parallel, elongated ramiform elements intergrade morphologically, and are characteristic of ozarkodinid conodont apparatuses (Aldridge et al., 1987; Sweet, 1988). Functionally, this group of elements was regarded by Hitchings and Ramsay (1978) to have served as a sieve basket, but was subsequently interpreted to have had a raptorial grasping function (Purnell, 1993b; Purnell and Donoghue, 1997). Norby (1976), using newly collected *L. commutatus* (= *L. commutata*) bedding-plane assemblages, recognized three distinct element types in Scott's "ten hindeodells," one A₃ (= S₀), two A_{1c} (= S₁), and six A₁ (= S_{2/3/4}) elements (Fig. 11.2); he did not differentiate an S₂ element.

As well as differentiating three types of A (= S) elements in the newly collected bedding-plane assemblages of *L. commutatus* (= *L. commutata*), Norby (1976) also determined that the

L. commutatus (= *L. commutata*) apparatus was composed of 15 elements, consisting of pairs of P (= P₁), O (= P₂), and N (= M) elements, as well as nine A (= S) elements. This conclusion was supported by Aldridge (1987) and Aldridge et al. (1987) when they determined that conodont apparatuses of the Polygnathacea Bassler, 1925, which includes *Lochriea commutata*, were composed of 15 elements. Each apparatus contained pairs of Pa (= P₁), Pb (= P₂), M, Sb, and Sd elements, two pairs of Sc elements, as well as an unpaired Sa (= S₀) element, which is an element plan that Purnell et al. (2000) determined to be plesiomorphic for complex conodonts. Purnell and Donoghue (1998) illustrated and described a bedding-plane assemblage of an unidentified species of *Lochriea* from the Namurian of Germany, the part and counterpart of which we re-illustrate in Figure 13.1 and 13.2, respectively. We also re-illustrate a camera lucida drawing of the same specimen (Fig. 14.1), first published by Purnell and Donoghue (1998), and subsequently amended by them to reflect topological element notation of Purnell et al. (2000). The three-dimensional apparatus architecture of the German *Lochriea* sp. specimen was illustrated by Purnell and Donoghue (1998, p. 76, figs. 11A, B) by juxtaposing a line drawing of *Lochriea* sp. with a photograph of a model of the apparatus architecture of another polygnathacean, identified by M. Purnell (personal communication, 2019) as being *Idiognathodus*, both here re-illustrated as Figure 14.1 and 14.2, respectively.

Our identification of 18 and 23 elements in the holotype and paratype, respectively, of *Lochriea montanaensis* Scott, 1942 (Fig. 1; Table 1) is clearly at odds with the apparatus composition of *Lochriea* spp. as determined by Norby (1976), von Bitter and Norby (1998a, b), and Purnell and Donoghue (1998). The anomalously high numbers of elements in the two assemblage specimens chosen by Scott (1942) as the primary types of *Lochriea montanaensis*, the presence of three and four each of the P₁, P₂, and M elements, and the anomalously high number of each of S_{3/4} and S elements in the holotype and paratype, respectively (Table 1), all suggest that the primary types consist of the elements of more than one individual. This, as well as their disorganized state (Fig. 1), suggests that both specimens are fecal composites, a conclusion at odds with those of Scott (1942, p. 293), who thought that the bedding-plane assemblages he was studying were not fecal, or accidental accumulations.

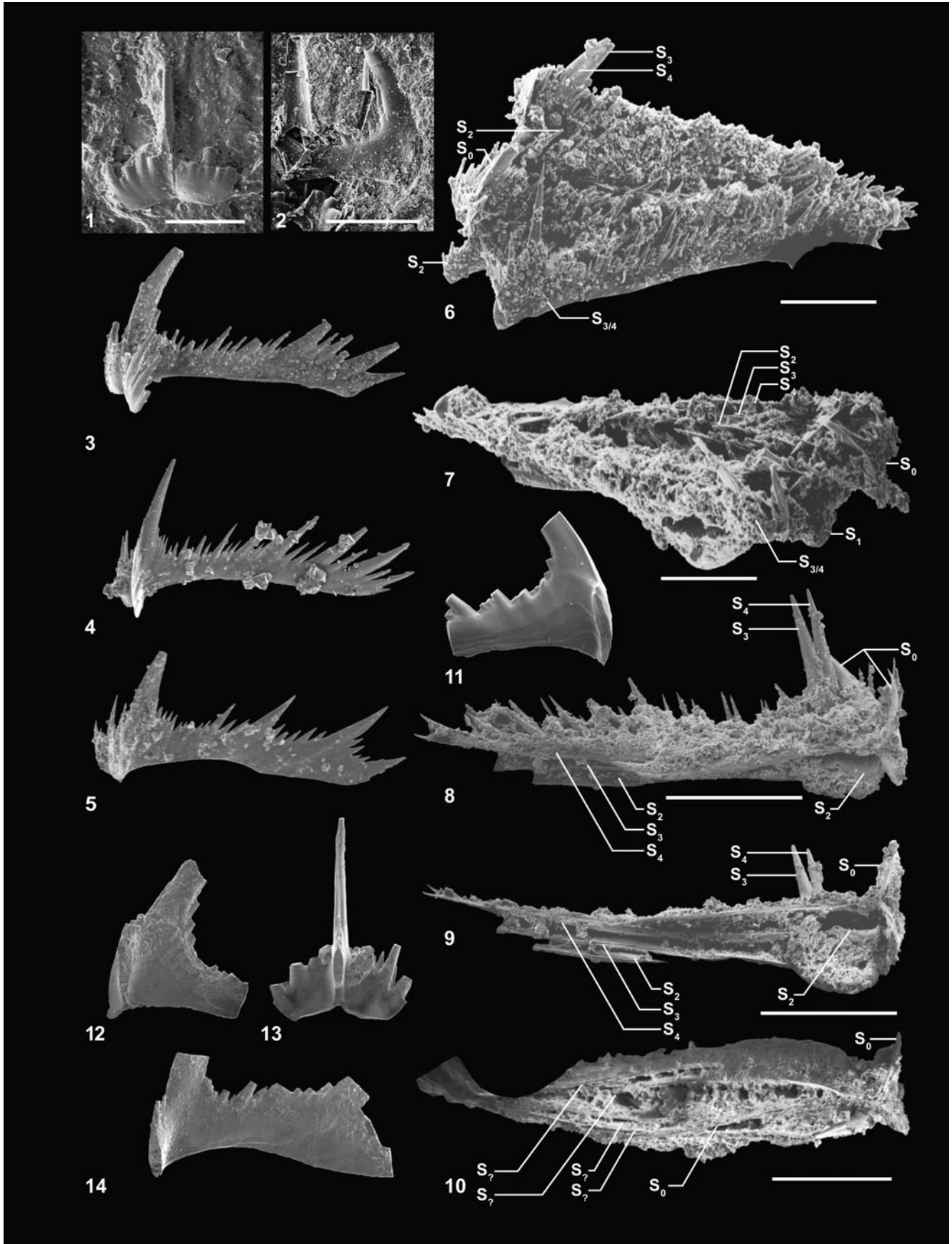


Figure 6. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) S_0 elements in bedding-plane assemblages (1, 2), as acid residue-derived discrete elements (3–5, 11–14), and in acid residue-derived fused assemblages (6–10). Scale bars (1, 2, 7–10) = 0.2 mm. For the remaining specimens, actual lengths are provided in descriptions below. (1) S_0 element, anterior view of anterolateral processes, with triangular bevel at base of cusp. Sample H-A-2-7-1, Heath Formation (not Tyler Formation as per Norby, 1976, pl. 11, fig. 15a), locality 2, Montana, USA, ISGS 62P-1103. (2) S_0 element, lateral dextral view of cusp and broken stubs of posterior and dextral anterolateral processes. See element 11 S_0 (Fig. 2.1B) for the apparatus context of this element. Sample H-B-1-B, Tyler Formation, locality 3, Montana, USA, ISGS 62P-207A. (3–5) S_0 elements, lateral sinistral views of an ontogenetic series showing a rarely preserved, long posterior process, and shorter sinistral and dextral anterolateral processes. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593945–593947. Horizontal lengths = 0.65, 0.55, and 0.50 mm, respectively. (6–10) S_0 elements, USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA. (6, 7) S_0 element in moderately complete sinistral and dextral fused S_{0-4} element array, lateral sinistral and dorsal views, respectively (see Fig. 5.5 for another view of this fused assemblage and of its S_0 element), USNM 593969. (8, 9) S_0 element with short symmetrical anterolateral processes and long posterior process in fused S element array, oblique dextroventral and ventral views, respectively, of the mostly sinistral side of the rostral apparatus, USNM 593970. (10) S_0 element with short symmetrical anterolateral processes and long posterior process in fused S element array, ventral view. Arcuate indentation in upper left is the outline of the scanning electron microscopy mounting medium. USNM 593971. (11) S_0 element, dextral view of broken anterolateral lateral and posterior processes, sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1104. Horizontal length = 0.51 mm. (12) S_0 element, sinistral view of broken anterolateral and posterior processes. Sample 5, Fayetteville Formation, locality 5, Oklahoma, USA, ISGS 82P-48. Horizontal length = 0.16 mm. (13) S_0 element, posterior view of symmetrical anterolateral processes and central stub of broken posterior process. Sample Schälk 50, Herdringen Formation, locality 10, North-Rhine Westphalia, Germany, ISGS 82P-49. Vertical height = 0.35 mm. (14) S_0 element, sinistral view of broken anterolateral process and moderately complete, but relatively short posterior process. Sample VS-4, Ridenhower Formation, locality 7, Illinois, USA, ISGS 62P-1208. Horizontal length = 0.46 mm.

The best preserved eight bedding-plane assemblages of *Lochriea commutata* collected by Norby (1976), and presented here, show a maximum of 15 elements (Fig. 2; Table 1). The presence of two each of the P_1 , P_2 , and M elements in all but two of the eight specimens, are in agreement with the number of these elements that other authors, including Norby (1976), Aldridge (1987), Aldridge et al. (1987), and Purnell and Donoghue (1997, 1998), concluded were present in ozarkonidid conodont apparatuses. Remarkably, the rarely identified S_0 element, even though not identified in the type specimens of *Lochriea montanaensis*, was recognized in three and possibly an additional two of the apparatuses of *Lochriea commutata* (Table 1). The presence of only a single M element in ISGS 62P-210 and possibly 62P-211 (Table 1) is likely due to either preservational factors, or to our inability to recognize this element. Similarly, we attribute the underrepresentation of one or more of the categories of S_1 , S_2 , and $S_{3/4}$ elements in these eight specimens (Table 1) to the same preservational and human factors, a reality that forced us to place anomalously large numbers of elements into the more generalized and less specific category of S elements (Table 1). The more balanced element maximum of up to 15 elements in the eight assemblages (Table 1) and their less disturbed distribution suggest that they are ‘natural’ bedding-plane assemblages.

That the type species of *Lochriea*, *L. commutata*, possessed a food processing apparatus of 15 elements (Norby 1976; von Bitter and Norby, 1998a, b) (Figs. 11.2, 12; Table 1) has provided, and continues to provide, an element blueprint for the apparatus of other *Lochriea* species. That reconstruction was supported and strengthened when Purnell and Donoghue (1998) documented the element composition of a well-preserved, but unidentified, species of *Lochriea* from the Namurian of Germany—a bedding-plane assemblage that, in an outline drawing updated by Purnell and Donoghue (personal communication, 2019), shows paired P_1 , P_2 , S_1 , S_2 , S_3 , and S_4 elements, as well as a single M element (a second M element was either not preserved, or was covered by other elements), and an S_0 element (Figs. 13.1, 13.2, 14.1).

The availability of an apparatus element blueprint for the type species *Lochriea commutata* resulted in others beginning to reconstruct the apparatuses of species of *Lochriea*, using a variety of approaches. The simplest approach was perhaps that of Stone (1991), who, using discrete collections, reconstructed

a partial *L. commutata* apparatus by identifying its P_a (= P_1), P_b (= P_2), M, and Sc_1 (= $S_{3/4}$) elements, based on criteria presented by Norby (1976). Another more complicated approach was that of Horowitz and Rexroad (1982), Varker (1994), and Nemyrovska et al. (2006), who assumed that one or more species of *Lochriea*, while distinguished by their P_a (= P_1) elements, each bore morphologically identical non-platform elements in their apparatuses. Thus Horowitz and Rexroad (1982), in reconstructing a partial apparatus of *L. commutata* from discrete faunas, assumed (text-fig. 10) that *L. mononodosa* bore the ‘same’ (i.e., morphologically identical) P_b (= P_2), M, and Sc (= $S_{3/4}$) elements as *L. commutata*, doing so despite the fact that the rare *L. mononodosa* P_a (= P_1) element was grouped in their cluster analysis in the middle of mostly elements of *Idioproniodus healdi* (Roundy, 1926) (Horowitz and Rexroad, 1982, text-fig. 3). Similarly, Varker (1994, p. 310) studying discrete elements and fused clusters, regarded *L. commutata*, *L. mononodosa*, and *L. nodosa* to “share” the same non- P_a elements (i.e., he interpreted the apparatuses of each of the three species to each have borne morphologically identical P_b [= P_2], M, S_a [= S_0], and Sc [= $S_{3/4}$] elements). Finally, Nemyrovska et al. (2006) concluded that the P_2 , M, and S elements of three species of *Lochriea* (*L. commutata*, *L. cracoviensis*, and *L. saharae*) were morphologically the same.

Assumptions of sharing non-platform elements in apparatuses of *Lochriea* spp., while possibly true, remain unproven, and there has been little success in reconstructing the apparatuses of *Lochriea* species, other than *L. commutata* (see Skompski et al., [1995] for a key to the up to 10 species of *Lochriea*, and to which additional species, such as *L. saharae* have since been added). The major reason for that lack of success is the relative rarity of bedding-plane assemblages and fused clusters of *Lochriea* spp., and that the reconstruction of conodont apparatuses from discrete collections is largely dependent on the availability of conodont faunas that are composed, if not of the elements of a single conodont species, then of the elements of several species, the components of which can readily be disentangled and identified.

The sole exception to our generalization that there have been few successful attempts to reconstruct the apparatuses of species other than that of *L. commutata*, involved five samples studied by Atakul-Özdemir et al. (2012, p. 1281) that contained “ P_1 elements of *L. homopunctatus* along with morphologically distinctive P_2 , M and S elements that could not be assigned to any of the 11 other co-occurring species.” These authors, in

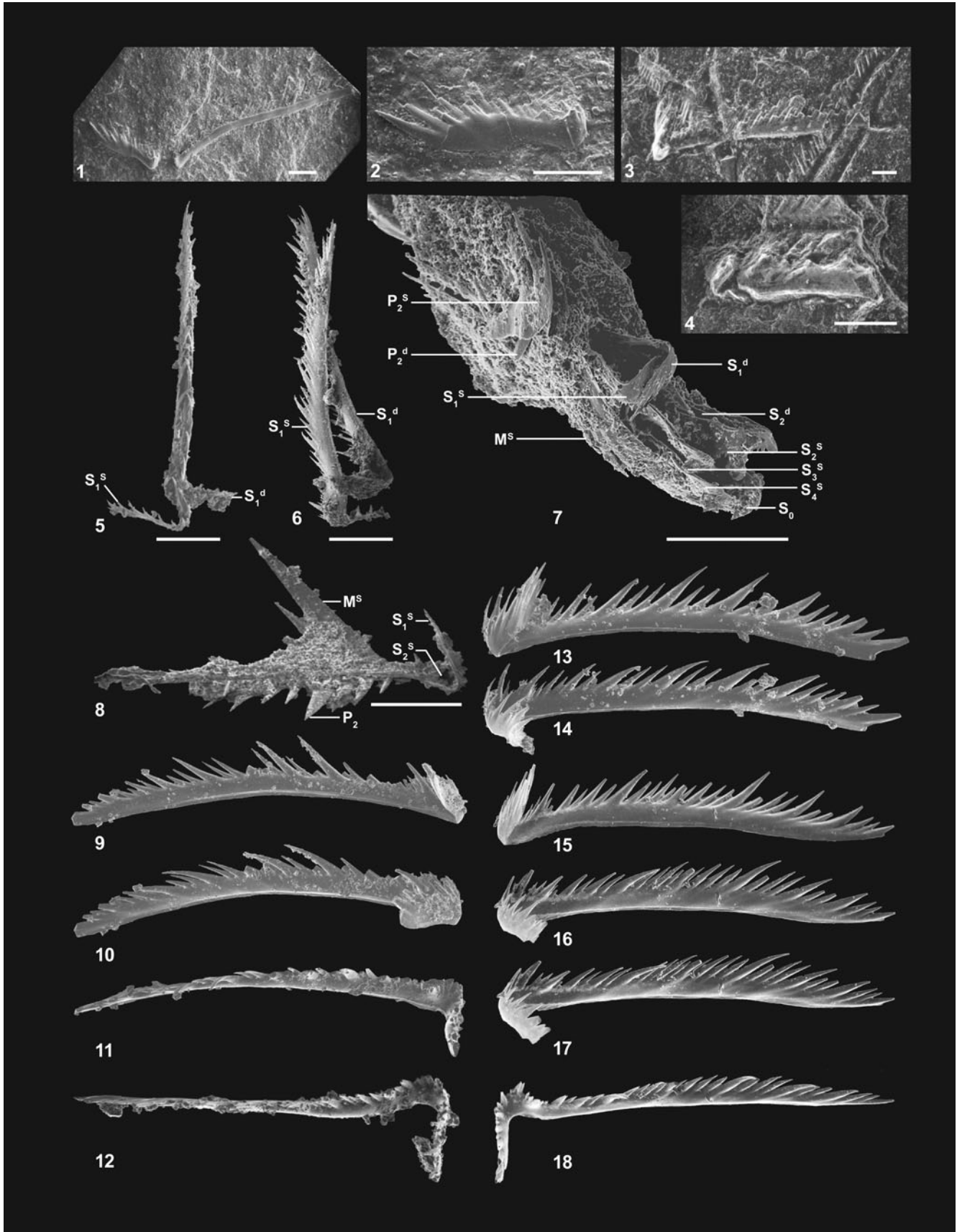


Figure 7. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) S_1 elements in bedding-plane assemblages (1–4), in acid residue-derived fused assemblages (5–8), and as acid residue-derived discrete elements (9–18). Scale bars (1–8) = 0.2 mm. For the remaining specimens, actual lengths are provided in descriptions below. (1, 2) S_1^s element with long posterior process in outer lateral view (1, right), and broken-off anterior process in outer lateral view (1, left, and 2). Sample H-A-2-2, Heath Formation, locality 2, Montana, USA, ISGS 62P-1114. (3) S_1^s element in outer lateral view, with an unidentified S element, a remnant of a possible M element crossing the posterior process and a possible P_2 element in upper left. See element 5 S_1^s (bottom of Fig. 2.5) for apparatus context of this element. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218A. (4) S_1^d element stub in inner lateral view. See element 11 S_1^d (upper Fig. 2.5) for apparatus context of this element. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218B. (5–8) S_1 elements in fused assemblages. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA. (5, 6) $S_1^{d,s}$ element pair in upper and lateral sinistral views, respectively; (6) is rotated around the rostrocaudal axis $\sim 90^\circ$ from (5), USNM 593972. (7) $S_1^{s,d}$ element pair in lower (ventral) view in moderately complete fused apparatus (see Figs. 4.8, 5.4 for other views of this element pair and of this fused cluster), USNM 593967. (8) S_1^s element in lower (ventral) view with its posterior process fused in functional position against posterior process of S_2^s element. Partially complete but disrupted apparatus, USNM 593973. (9–18) S_1 elements, acid residue-derived discrete elements. USGS collection 34004-PC, Bluestone Formation, location 8, West Virginia, USA. (9–11) S_1^s element in inner views (9, 10) and in upper view (11), USNM 593948. Length = 1.18 mm. (12) S_1^s element in upper view, USNM 593949. Length = 0.76 mm. (13, 14) S_1^d element in inner views, USNM 593950. Length = 0.90 mm. (15–18) S_1^d element tilted to varying degrees in inner views (15–17) and in upper view (18), USNM 593951. Length = 0.93 mm.

reconstructing most of the apparatus of *L. homopunctatus*, also concluded that the characteristics of P_2 , M, and S elements may be as, or more, important in determining and defining *Lochriea* spp. than those of the traditionally used P_1 elements. We concur and contend that the current practice of assigning species to *Lochriea* almost entirely on the basis of ornamented or unornamented P_1 elements leaves those assignments in doubt, at least until the rest of their apparatuses are determined, and found to be similar to that of the type species. Relying solely on P_1 elements to carry the taxonomy ignores important taxonomic and phylogenetic information that almost certainly resides in the other elements of their apparatuses. Of interest in this context, and a step forward, was the interpretation by Atakul-Özdemir et al. (2012) of an M element, illustrated by Nemyrovskaya et al. (2006) from a sample from Algeria containing P_1 elements of only a single *Lochriea* species, *L. saharae*, as the M element of that species.

Materials and methods

We studied three kinds of conodont fossils, the first, and the most commonly recovered, being individual discrete elements that collectively functioned in the feeding apparatuses of conodonts. Isolated discrete elements were recovered from carbonates or carbonate-rich sediments by standard acid digestion techniques, using either dilute acetic or formic acid (Collinson, 1963, 1965; Stone, 1987) and from organic-rich black shales using a sodium hypochlorite and sodium hydroxide solution (Norby, 1976; Duffield and Warshauer, 1979; Stone, 1987) and Stoddard Solvent, a kerosene-derivative, used to process soft clay-rich shales (Collinson, 1963, 1965; Norby, 1976). Gentle boiling in water with Quaternary O, a deflocculating agent, was used for all shales and some carbonates (Norby, 1976; Duffield and Warshauer, 1979; Stone, 1987). Discrete elements were concentrated using heavy liquids such as tetrabromoethane (Collinson, 1963, 1965; Stone, 1987), then the heavy fractions, occasionally magnetically separated, were subsequently hand-picked for conodont elements using binocular microscopes.

The second, much less common material collected and studied, are bedding-plane assemblages, most commonly preserved on black shale surfaces as groups of conodont elements preserved in close proximity to one another, that are either classified as fecal assemblages, or as natural assemblages, depending on whether or not they had been ingested and gone through the gut of a conodontophage. In rare situations, a conodont assemblage inside the body of a conodontophage is both

sufficiently well preserved, and retains enough of its original structure, to be classified as a natural assemblage, one such example being the apparatus of the conodont *Kladognathus Rexroad, 1958*, in the midgut of the conodontophage *Typhloesus wellsi* (Melton and Scott, 1973), and another is the apparatus of the conodont *Bispathodus Müller, 1962* in the gut of a Devonian shark (Purnell and Donoghue, 1998).

In this study, bedding-plane assemblages were recovered by hand splitting organic-rich black fissile shales with a thin sharp knife or a cleaver, and then using the naked eye and a hand-lens or a low-powered microscope to locate them; the latter procedure was best accomplished by taking advantage of the reflectivity of the conodont elements in the sun in the field, or of artificial light in the laboratory. The most useful natural assemblages were, and are, those that had not been disturbed, or had only been minimally disturbed, by sedimentologic, taphonomic, or biologic processes, and that preserved important information regarding the number, morphological types, and arrangement of conodont elements in the feeding apparatus of conodonts. Conversely, feeding apparatuses that had been ingested, digested, and excreted, generally preserved a minimum of such information.

The third, and the rarest kind of conodont material studied, were fused clusters, which, depending on their history and on their preservation, may be considered more three-dimensional categories of bedding-plane assemblages, also theoretically being divisible into both ‘natural’ and ‘fecal’ categories. In fused clusters, typically just the elongated bipennate elements are compacted and fused together, and are preserved in their original relative position and orientation within the feeding apparatus. The fused clusters of *Lochriea commutata* recovered and studied by us are only the second reported occurrence, after Varker (1994), of fused clusters of *Lochriea* spp. The fused clusters were recovered from carbonate concretions by the standard acid digestion and heavy liquid techniques described above.

Our examination of Scott’s (1942) *Lochriea montanaensis* bedding-plane assemblages suggests that although some represent the feeding apparatus of a single individual and provide information regarding the element composition of the *L. commutata* feeding apparatus, all appear to be of fecal origin (Fig. 1; Table 1). In contrast, we subjectively categorize the 34 bedding-plane assemblages of *L. commutatus* (= *L. commutata*) collected by Norby (1976) from the Heath Formation of Montana, as three natural, two ?natural, 23 fecal, and six ?fecal. Similarly, of the 81 assemblages collected by Norby (1976) from the Tyler Formation of Montana, we categorize five as natural, 29 as ?natural, 19 as fecal, and 28 as ?fecal.

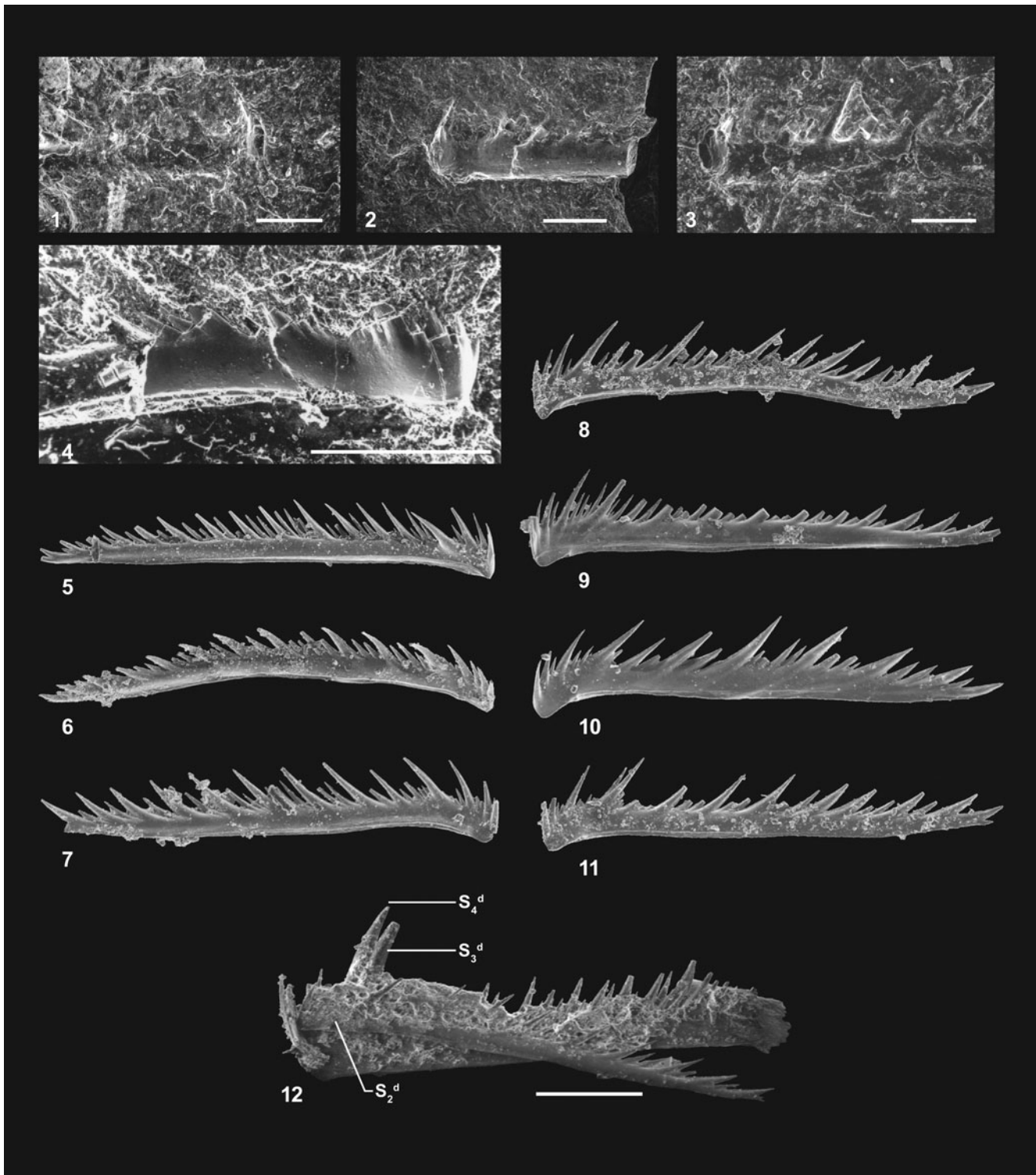


Figure 8. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) S₂ elements in bedding-plane assemblages (1–4), as acid residue-derived discrete elements (5–11), and in an acid residue-derived fused assemblage (12). Scale bars (1–4, 12) = 0.2 mm. For the remaining specimens, actual lengths are provided in descriptions below. (1, 2) ?S₂^d element in inner lateral view of anterior end of part and counterpart, respectively. See element 10?S₂^d (lower and upper Fig. 2.5, respectively), for apparatus context of this element. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218A and 62P-218B. (3) ?S₂^s element in inner view; see element 9?S₂^s (lower Fig. 2.5) for apparatus context of this element. Sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218A. (4) ?S₂^d element, *Lochriea montanaensis* Scott, holotype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]) in outer view of anterior end; see element 6?S₂^d (Fig. 1.1, 1.2) for apparatus context of this element. Heath Formation, locality 2, Montana, USA, UI X-1318. (5–11) S₂^s elements (5–7) and S₂^d elements (8–11) in inner views of two partial ontogenetic series. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593952–593958. Lengths = 1.13, 1.01, 0.86, 1.05, 1.02, 0.74, and 0.76 mm, respectively. (12) S₂^d element in inner view, fused against the inner surface of an S₃^d element, which is, in turn, fused against the inner surface of an S₄^d element. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593974.

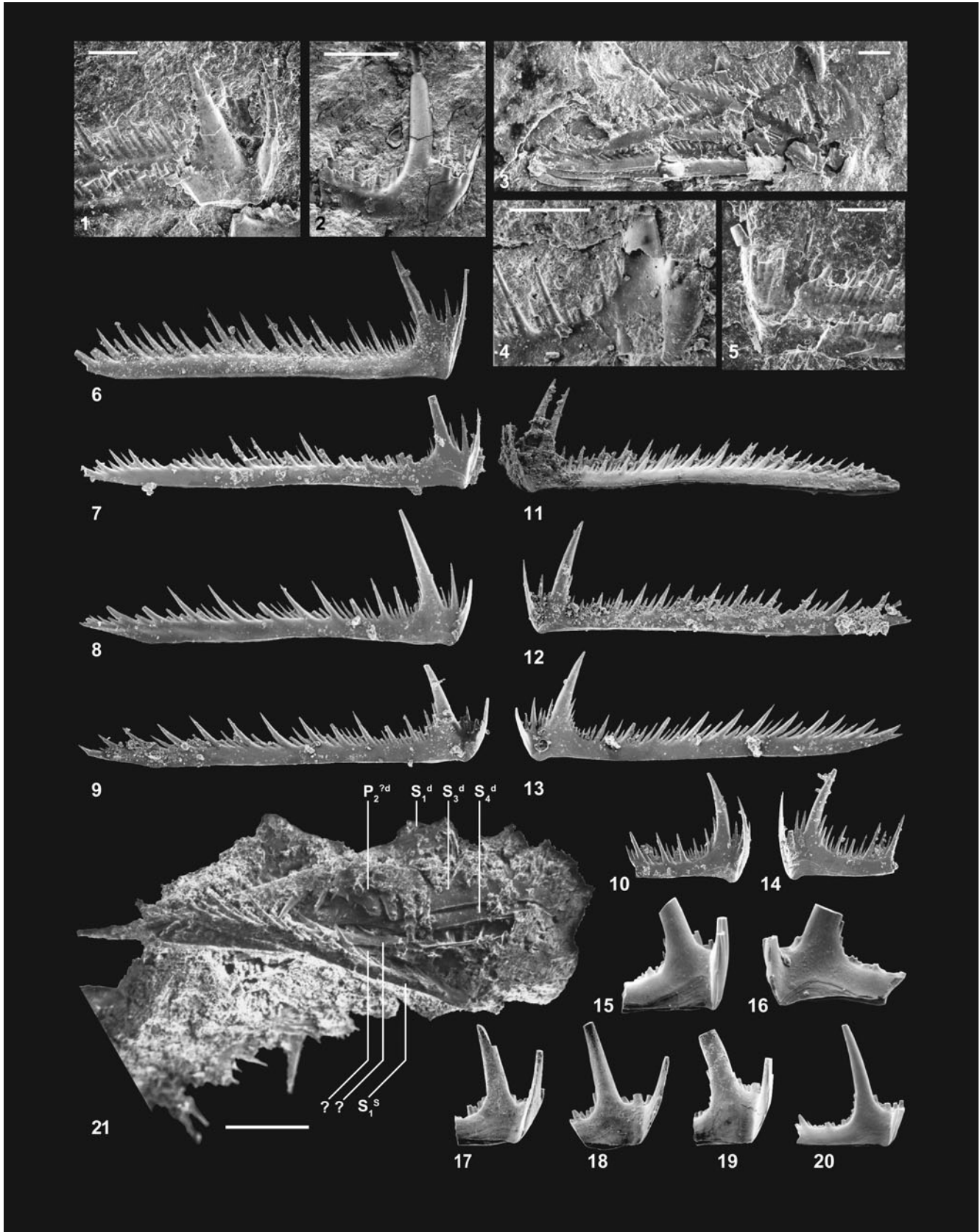


Figure 9. *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) $S_{3/4}$ elements in bedding-plane assemblages on shale surfaces (1–5), as acid residue-derived discrete elements (6–10, 12–20), and in acid residue-derived fused assemblages (11, 21). Scale bars (1–5, 21) = 0.2 mm. For the remaining specimens, actual lengths are provided in descriptions below. (1, 5) S_3^s and S_4^s element pair in inner views of part and counterpart, respectively. S_3^s element closest to viewer lacks most of posterior process, whereas S_4^s element behind S_3^s element is only an impression; see elements 7 S_3^s and 8 S_3^s (Fig. 2.5) for apparatus context of this element pair; sample H-A-2-7-1, Heath Formation, locality 2, Montana, USA, ISGS 62P-218A and 62P-218B. (2) $S_{3/4}^d$ element, *Lochriea montanaensis* Scott, paratype (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]) in outer lateral view of anterior end; see element 1 $S_{3/4}^d$ (Fig. 1.3, 1.4) for apparatus context of this element. Heath Formation, locality 2, Montana, USA, UI X-1319. (3, 4) $S_{3/4}^d$ element in outer view in S element array. Anterior end of $S_{3/4}^d$ element in upper right, posterior end in lower left of (3); close-up of anterior end of $S_{3/4}^d$ element in (4) (see element 12 $S_{3/4}^d$ in Fig. 2.1B for apparatus context of this and associated elements 11 S_0 and 13 S_3^s). Sample H-B-1-B, Tyler Formation, locality 3, Montana, USA, ISGS 62P-207A. (6–10) $S_{3/4}^s$ elements in inner lateral views, forming a partial ontogenetic growth series. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593959–593961, 696951, 593962. Lengths = 1.44, 1.45, 1.21, 1.28, and 0.49 mm, respectively. (11) S_3^d and S_4^d element pair in inner view in partial fused assemblage; outer surface of S_3^d element fused in functional position against inner surface of S_4^d element (see Fig. 8.12 for an almost identical S_3^d and S_4^d element pair, except for the additional presence of an S_2^d element). USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 696952. Length = 1.16 mm. (12–14) $S_{3/4}^d$ elements in inner views, that together with USNM 696952 (11) form a partial ontogenetic growth series. USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USA, USNM 593963–593965. Lengths = 1.31, 1.00, and 0.45 mm, respectively. (15–20) $S_{3/4}^s$ elements in inner views of anterior ends. (15) $S_{3/4}^s$ element. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1109. Length = 0.48 mm. (16) $S_{3/4}^s$ element. Sample H-B-1-A, Tyler Formation, locality 3, Montana, USA, ISGS 62P-1107. Length = 0.29 mm. (17) $S_{3/4}^s$ element. Sample 5, Fayetteville Formation, locality 5, Afton, Oklahoma, USA, ISGS 82P-50. Height = 0.21 mm. (18) $S_{3/4}^s$ element. Sample 5, Fayetteville Formation, locality 5, Afton, Oklahoma, USA, ISGS 82P-51. Height = 0.24 mm. (19) $S_{3/4}^s$ element. Sample Schälk 50, Herdringen Formation, locality 10, North-Rhine Westphalia, Germany, ISGS 82P-52. Height = 0.25 mm. (20) $S_{3/4}^s$ element. Sample VS-7, Ridenhower Formation, locality 7, Illinois, USA, ISGS 62P-1209. Length = 0.38 mm. (21) $S_{3/4}^s$ pair in ?upper (?dorsal) view of partial S element array (see Fig. 3.35 for another view of this fused cluster). USGS collection 34004-PC, Bluestone Formation, locality 8, West Virginia, USNM 593966.

Several of the Montana natural assemblages of *L. commutata* are shown on Figure 2. Those considered natural consist of up to 15 elements, although some elements may be hidden beneath other elements. Natural assemblages typically exhibit a recognizable recurring pattern of element positions; however, element positions may be disrupted by post-mortem changes. Those assemblages termed ?natural are probably natural, but show varying degrees of element disturbance; these two categories provide the most useful information regarding original element composition and position. Fecal assemblages are associations of two or more elements, but typically of 15 or more elements of varying maturities, sometimes including elements belonging to different conodont species, that are jumbled, show no discernible element pattern, and occur with black bituminous material. Assemblages termed ?fecal are most likely fecal, however, they typically may represent one, or sometimes two or more relatively complete individuals, that show moderate to significant disruption. They occasionally provide information regarding element composition and position in an apparatus. Conodonts in the fecal and ?fecal categories were either regurgitated, excreted, or even brought together by bottom currents.

We list the material studied by locality in the section that follows. Abbreviations for the institutions at which specimens are repositated are provided at the end of the section, and locality data are provided in the Appendix.

Locality 1 (Heath Formation, Montana).—One partial bedding-plane assemblage (CM 33965) and several isolated elements of *L. commutata* collected by Richard Lund.

Locality 2 (Heath Formation, Montana).—Two bedding-plane assemblages collected by Scott (1942), and designated by him as holotype and paratype of *L. montanaensis*, UI X-1318 and UI X-1319, respectively. Forty-nine bedding-plane assemblages and dozens of isolated elements on shale surfaces designated as *L. montanaensis* paratypes on UI slides; none assigned numbers by Scott (1942). Scott (1942) reported that he recovered 180 conodont assemblages and 3,000 individual elements from Montana, but most of these specimens could not be located at UI.

Thirty-four bedding-plane assemblages of *L. commutata* (*L. montanaensis*) and more than a thousand topotype P_1 , P_2 , M , S_0 , S_1 , S_2 , and $S_{3/4}$ elements collected by Norby (1976), and repositated at the ISGS.

Locality 3 (Tyler Formation, Montana).—Eighty-one bedding-plane assemblages and several thousand P_1 , P_2 , M , S_0 , S_1 , ? S_2 , and $S_{3/4}$ elements of *L. commutata* collected by Norby (1976), and repositated at the ISGS.

Locality 4 (Hindsville Formation, Oklahoma).—The syntype of *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) (UM C552-2) selected by von Bitter and Norby (1994a) as the lectotype of *S. commutatus*, and here as the lectotype of *L. commutata*. Topotype *L. commutata* P_1 , P_2 , M , S_0 , and $S_{3/4}$ elements collected by RDN and repositated at the ISGS.

Locality 5 (Fayette Formation, Oklahoma).—*Lochriea commutata* P_1 , M , S_0 , and $S_{3/4}$ elements collected by RDN and repositated at the ISGS.

Locality 6 (Goddard Formation, Oklahoma).—*Lochriea commutata* P_1 element (SUI 33624) illustrated by Lane and Straka (1974, fig. 37.1, 37.2).

Locality 7 (Ridenhower Formation, Illinois).—*Lochriea commutata* P_1 , P_2 , M , S_0 , and $S_{3/4}$ elements collected by RDN and repositated at the ISGS.

Locality 8 (Bluestone Formation, West Virginia).—Fused clusters and P_1 , P_2 , M , S_0 , S_1 , S_2 , and $S_{3/4}$ elements of *L. commutata* collected by RGS and repositated at the USNM.

Locality 9 (Upper Windsor Group, Nova Scotia).—*Lochriea commutata* P_1 , P_2 , and M elements collected by PvB and repositated at the ROM.

Locality 10 (Herdringen Formation, Germany).—*Lochriea commutata* P_1 , M , S_0 , and $S_{3/4}$ elements collected by Charles

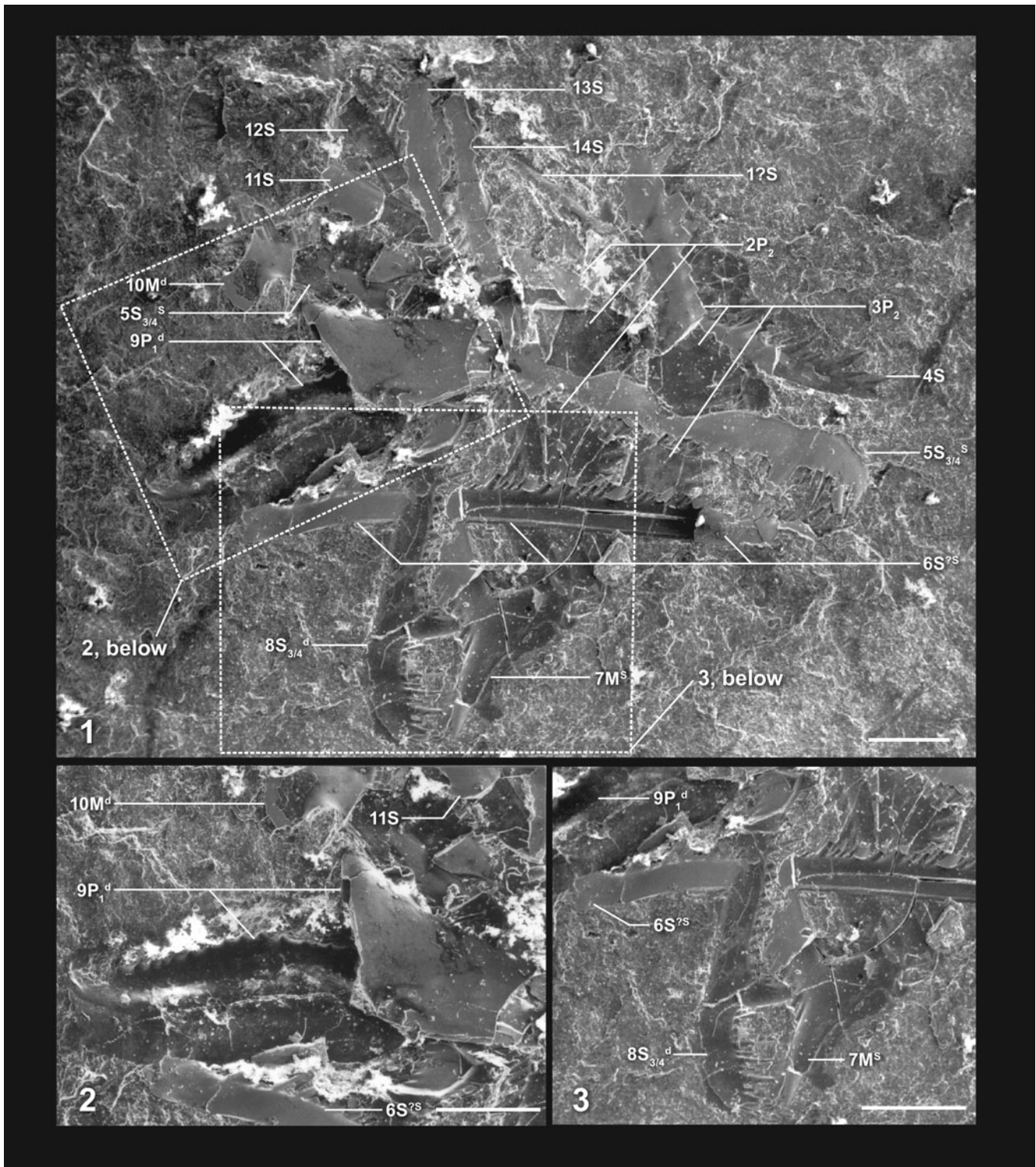
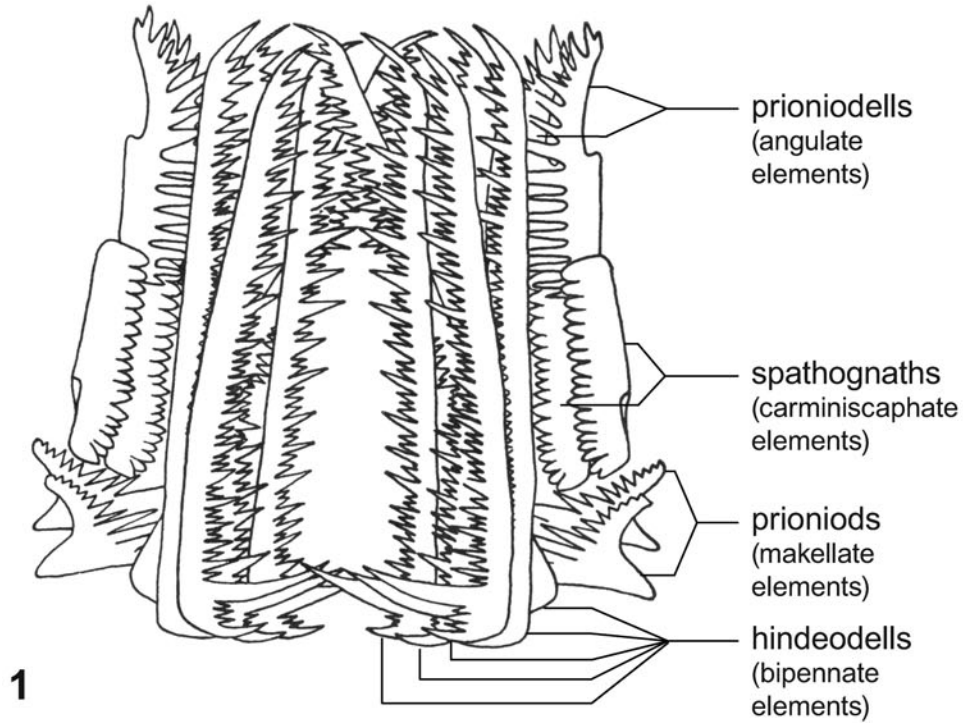


Figure 10. *Lochriea bigsnowyensis* Scott, 1942, holotype (= an undetermined species of *Cavusgnathus* Harris and Hollingsworth, 1933), illustrated by Scott (1942, pl. 38, fig. 8); paratype UI X-1321 lost. No counterpart known. Scanning electron micrographs of bedding-plane assemblage on black shale, with interpretation of conodont elements present. All elements, notably the P_1^d element ($9P_1^d$), are characteristic of species of *Cavusgnathus* Harris and Hollingsworth, 1933. Heath Formation, locality 2, Montana, USA, UI X-1320. Scale bars = 0.5 mm. (1) Fecal assemblage of 14 elements numbered clockwise commencing in upper right. (2) The carminisclaphate P_1^d element and parts of associated M and S elements. (3) M and S elements below P_1^d element.

Collinson and reposit at the ISGS. P_1 elements from this locality were previously documented and referred to by von Bitter and Norby (1994a, b).

Locality 11 (Lüsenberg Formation, Germany).—Part and counterpart of bedding-plane assemblage of *Lochriea* sp. (IMGP Gö 600-36) from the collection of Schmidt and Müller



Taxon	Shape	Shape			
		carminiscaphate	angulate	makellate	alate and bipennate
<i>Lochriea montanaensis</i> Scott, 1942		spathognaths 4	prioniodells 4	prioniods 4	hindeodells 10+
<i>Lochriea wellsii</i> Melton and Scott, 1973	U of M 6027	spathognathodids –	ozarkodinids –	neoprioniodids 1	hindeodellids 9+
	U of M 6028	1	–	3	12
<i>Lochriea wellsii</i> Melton and Scott, 1973 (Scott, 1973)		platform-type 3?	ozarkodinids 1?	neoprioniodids 3?	hindeodellids 10 (in text gave range of 8-16)
<i>Lochriea commutatus</i> (Branson and Mehl, 1941) (Branson and Mehl, 1941b) (Norby, 1976)		P 2	O 2	N 2	A ₃ 1 A _{1c} 2 – A ₁ 6
<i>Lochriea commutata</i> (Branson and Mehl, 1941) (Branson and Mehl, 1941b) (von Bitter and Norby, 1998)		Pa 2	Pb 2	M 2	Sa 1 Sb ₁ 2 Sb ₂ 2 Sc 4
<i>Lochriea</i> sp. Purnell and Donoghue, 1998		Pa 2	Pb 2	M 2	Sa 1 Sb ₁ 2 Sb ₂ 2 Sc ₁ 2 / Sc ₂ 2
<i>Lochriea commutata</i> (Branson and Mehl, 1941) (Branson and Mehl, 1941b) (This paper, using topological element notation of Purnell et al., 2000)		P ₁ 2	P ₂ 2	M 2	S ₀ 1 S ₁ 2 S ₂ 2 S _{3/4} 2 / S _{3/4} 2

2

Figure 11. (1) Twenty-two (22⁺) element apparatus reconstructions of *Lochriea montanaensis* Scott, a subjective junior synonym of *L. commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b); after Scott (1942) and labeled with his terminology for the four element types recognized by him; shape categories used (in parentheses) are those of Sweet (1981, 1988). (2) Interpretations of the apparatus composition of *Lochriea* spp. since 1942, based on bedding-plane assemblages. *Lochriea wellsii* was named for a conodontophage containing elements of species of *Lochriea* and other conodont taxa in its gut. The identity of *Lochriea* sp. of Purnell and Donoghue (1998) is indeterminate, and the reconstruction of *L. homopunctatus* (Ziegler, 1960) by Atakul-Özdemir et al. (2012), based on discrete elements, is not included.

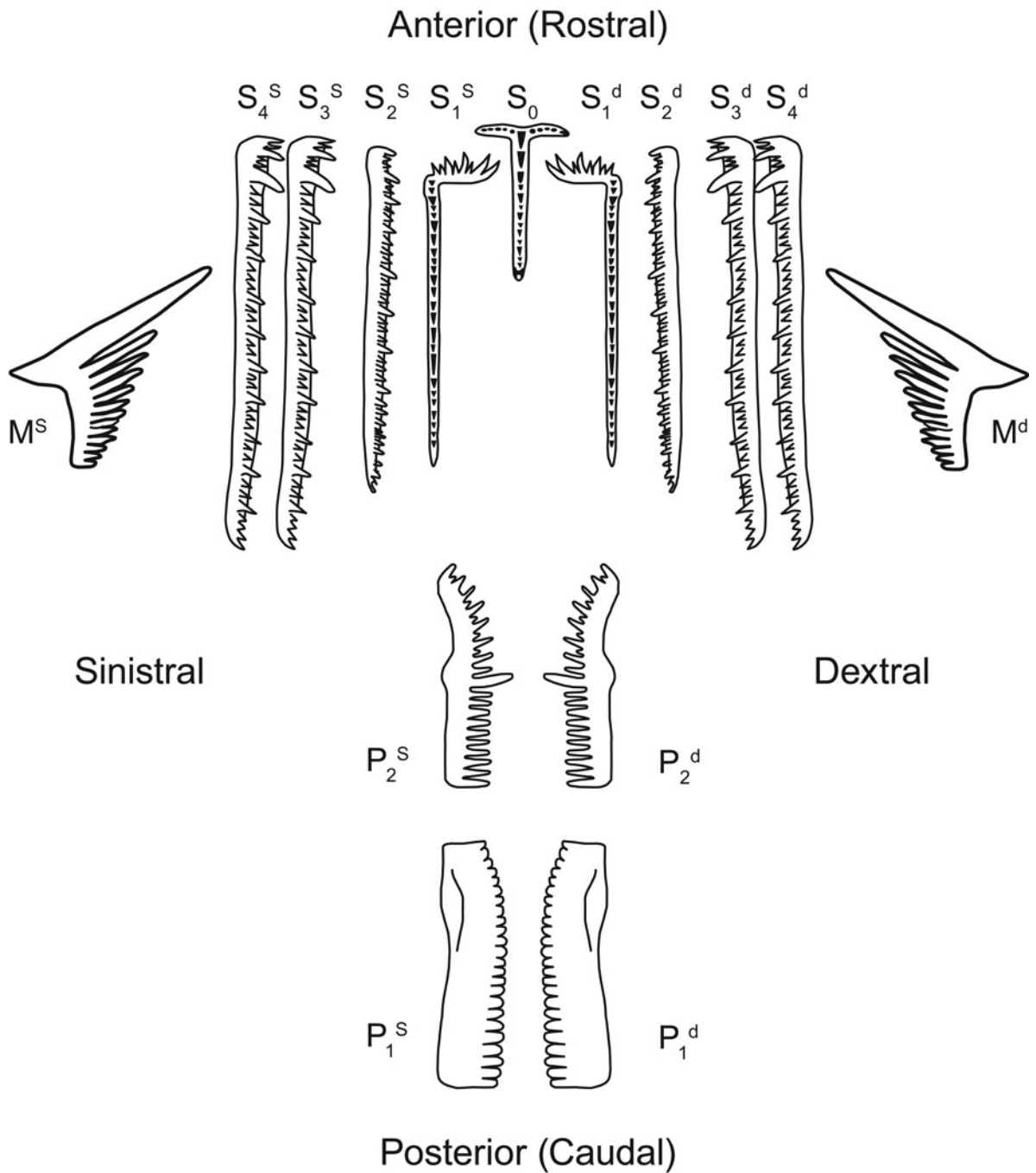


Figure 12. The 15 element apparatus of *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) in exploded view using the topological element notation of Purnell et al. (2000; cf., their fig. 3). This two-dimensional diagrammatic representation of the three-dimensional apparatus shows the apparatus in dorsal view, but does not show the downward (ventrally) sloping anterior (rostral) ends of the S elements or the vertical (dorsoventral) orientation of the P element pairs, whose anterior ends point downward (ventrally). Morphologically, P₁ elements are carminiscaphate, P₂ elements are angulate, M elements are makellate, the S₀ element is alate, and S₁–S₄ elements are bipennate with three different morphologic types.

(1964), illustrated by Purnell and Donoghue (1998). Original material not examined; only photographs studied.

Notes on conodont element notation.—*Lochriea commutata* Scott, 1942, *Lochriea* sp. of Purnell and Donoghue (1998), and *Lochriea bigsnowyensis* Scott, 1942, the latter here re-assigned to *Cavusgnathus* Harris and Hollingsworth, 1933,

possessed 15-element apparatuses of paired P₁, P₂, M, S₁, S₂, S₃, and S₄ elements, and an unpaired S₀ element. Many of the illustrated elements of these taxa have a superscript notation d, ?d, s, or ?s after the element type, indicating whether that element was positioned on the right (dextral) or the left (sinistral) side of the plane of bilateral symmetry of the skeletal apparatus (Sweet, 1981), with the question mark

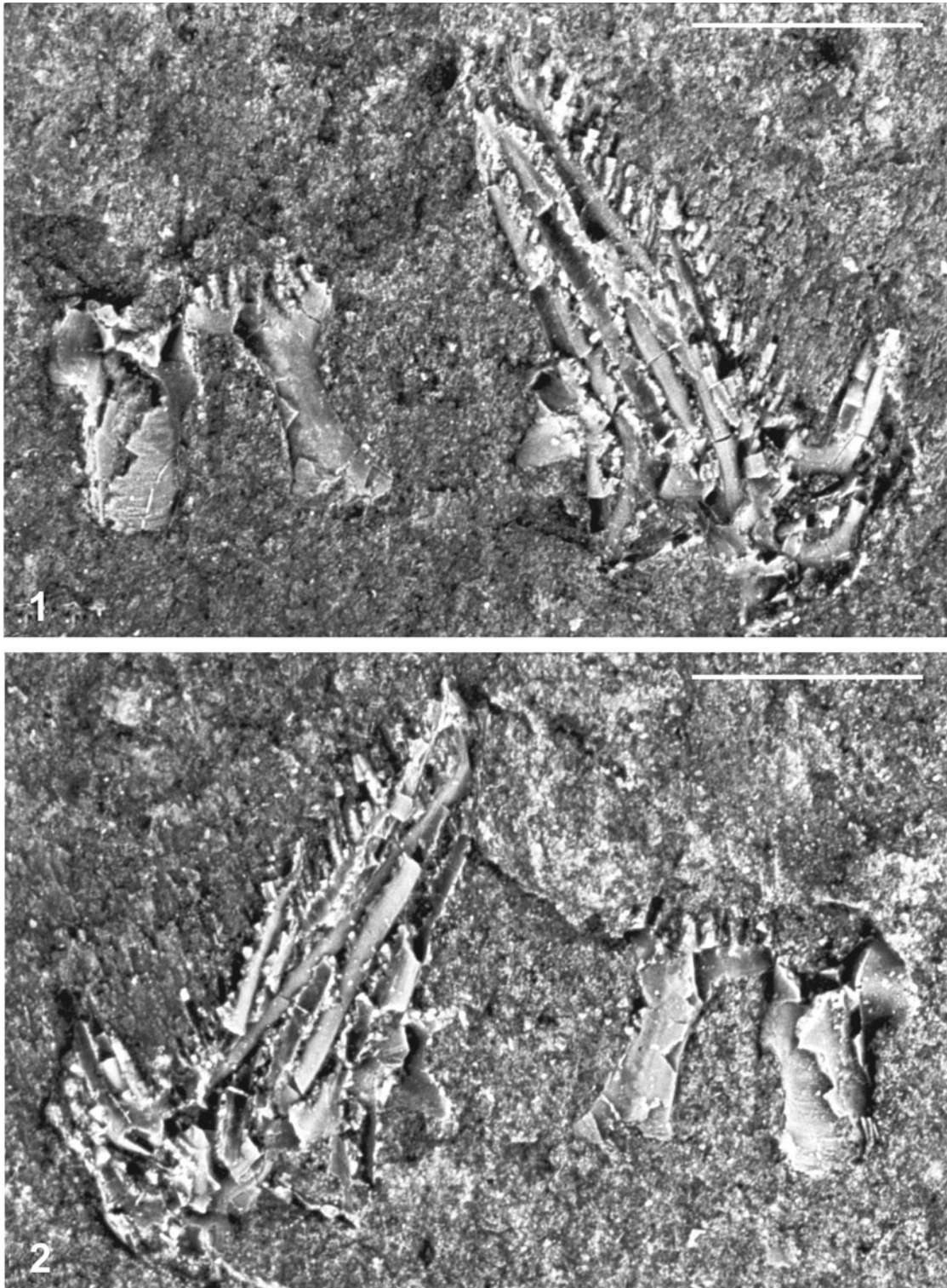


Figure 13. *Lochriea* sp. bedding-plane assemblage, counterpart (1) and part (2), as designated by Purnell and Donoghue (1998, pl. 2). Lüssenberg Formation, locality 11, North-Rhine Westphalia, Germany, IMG P Gö 600-36. From the collection of Schmidt and Müller (1964); after Purnell and Donoghue (1998, pl. 2), and reproduced with permission of the Palaeontological Association. Scale bars = 1 mm.

indicating uncertainty (e.g., a P_2^d element is a dextral P_2 angulate element positioned on the right side of the feeding apparatus, and a $S_2^{?s}$ element is a questionable sinistral S_2 bipennate element on the left side of the apparatus).

Repositories and institutional abbreviations.—Specimens examined in this study are deposited in the following institutions: Carnegie Museum of Natural History (CM), Pittsburg, Pennsylvania, USA; University of Göttingen (IMG P

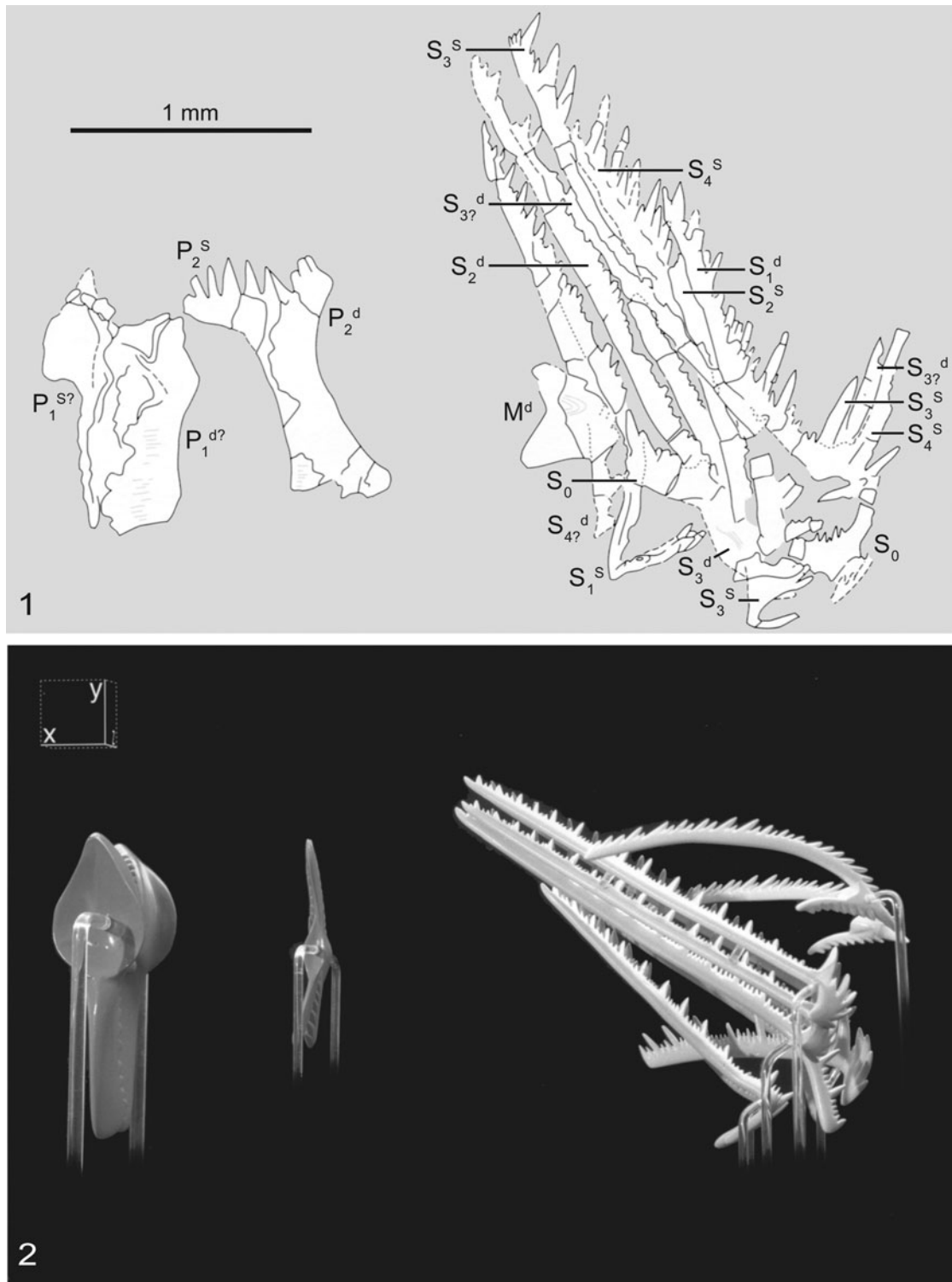


Figure 14. (1) *Lochriea* sp., bedding-plane assemblage, composite camera lucida drawing of IMGP Gö 600-36 (counterpart) shown in Figure 13.1. After Purnell and Donoghue (1998, text-fig. 11A), and reproduced with permission the Palaeontological Association. Positional element notation shown was modified and provided by M. Purnell subsequent to the publication of Purnell and Donoghue (1998), and is used with their permission. (2) Photograph of a model, identified by M. Purnell (personal communication, 2019) as of *Idiognathodus* sp., taken from right side and slightly in front to simulate the collapse pattern of *Lochriea* sp. shown in Figures 13 and 14.1. After Purnell and Donoghue (1998, text-fig. 11B), and reproduced with permission of the Palaeontological Association.

Gö), Göttingen, Germany; Illinois State Geological Survey (ISGS), Champaign-Urbana, Illinois, USA; Royal Ontario Museum (ROM), Toronto, Ontario, Canada; State University

of Iowa (SUI), Iowa City, Iowa, USA; University of Illinois (UI), Champaign-Urbana, Illinois, USA; University of Missouri (UM), Columbia, Missouri, USA; University of

Table 1. Conodont elements on the holotype and paratype of *Lochriea montanaensis* Scott, 1942 (= *Lochriea commutata* [Branson and Mehl, 1941] [Branson and Mehl, 1941b]) from the Heath Formation, and on three and five specimens of *Lochriea commutata* (Branson and Mehl, 1941) (Branson and Mehl, 1941b) from the Heath and Tyler formations, respectively. All 10 specimens are bedding-plane assemblages from Montana, USA. Underlined element designations (i.e., $\underline{3P_1}$, $\underline{3P_2}$, $\underline{3M}$, $\underline{2S_1}$, $\underline{1S_2}$, $\underline{6S_{3/4}}$, etc.) are the number of each those elements identified on that assemblage. The parenthetical designations below them—($2P_1^s$, $3?P_1$, $11P_1^{?d}$), ($4P_2$, $13P_2^{?s}$, $17P_2^{?d}$), and so forth—represent the position of that element in that assemblage, as labeled on Figures 1 and 2, followed by our determination of the identity of that element, preceded or followed by question marks indicating the degree of certainty of our identification. An asterisk (*) indicates only the part is present; other conodont elements may have been present on the counterpart.

[= <i>Lochriea commutata</i> [Branson and Mehl, 1941] [Branson and Mehl, 1941b)] assemblage specimen	Total identified	Number of elements							S (indeterminate or unidentifiable)
		P_1	P_2	M	S_0	S_1	S_2	$S_{3/4}$	
Holotype of <i>Lochriea montanaensis</i> Scott, 1942 UI X-1318 (Fig. 1.1, 1.2)	18	$\underline{3P_1}$ ($2P_1^s$, $3?P_1$, $11P_1^{?d}$)	$\underline{3P_2}$ ($4P_2$, $13P_2^{?s}$, $17P_2^{?d}$)	$\underline{3M}$ ($8M^d$, $9M^s$, $18M^d$)		$\underline{2S_1}$ ($10S_1^{?s}$, $16S_1^s$)	$\underline{1S_2}$ ($6?S_2^d$)	$\underline{6S_{3/4}}$ ($1?S_{3/4}^{?s}$, $5?S_{3/4}$, $7?S_{3/4}^{?s}$, $12S_{3/4}$, $14?S_{3/4}^{?d}$, $15S_{3/4}^d$)	
Paratype of <i>Lochriea montanaensis</i> Scott, 1942 UI X-1319 (Fig. 1.3, 1.4)	23	$\underline{4P_1}$ ($6P_1^{?d}$, $10P_1^{?s}$, $19?P_1$, $21P_1$)	$\underline{4P_2}$ ($4P_2$, $7P_2^{?s}$, $9?P_2$, $16P_2$)	$\underline{4M}$ ($8M^s$, $14M^s$, $15M^d$, $20?M$)		$\underline{1S_1}$ ($23?S_1^d$)		$\underline{4S_{3/4}}$ ($1S_{3/4}^d$, $2S_{3/4}^d$, $11S_{3/4}^s$, $18S_{3/4}^d$)	$\underline{6S}$ ($3S$, $5S$, $12S$, $13S$, $17S$, $22S$)
ISGS 62P-207 (Fig. 2.1A, B)	15	$\underline{2P_1}$ ($1P_1^s$, $2P_1^d$)	$\underline{2P_2}$ ($4P_2^d$, $5P_2^s$)	$\underline{2M}$ ($14?M$, $15M^d$)	$\underline{1S_0}$ ($11S_0$)	$\underline{2S_1}$ ($3?S_{1/2}$, $13?S_1^s$)		$\underline{1S_{3/4}}$ ($12S_{3/4}^d$)	$\underline{5S}$ ($6?S$, $7S$, $8S$, $9S$, $10S$)
ISGS 62P-216 (Fig. 2.2, 2.3)	15	$\underline{2P_1}$ ($1P_1^{?s}$, $2P_1^{?d}$)	$\underline{2P_2}$ ($3P_2^{?s}$, $4P_2^{?d}$)	$\underline{2M}$ ($10M^d$, $15M^s$)	$\underline{1S_0}$ ($12S_0$)	$\underline{2S_1}$ ($7S_1^s$, $11S_1^d$)	$\underline{1S_2}$ ($8?S_2$)	$\underline{2S_{3/4}}$ ($6S_{3/4}^d$, $9S_{3/4}^d$)	$\underline{3S}$ ($5S$, $13S$, $14S$)
ISGS 62P-215 (not figured)	15	$2P_1$	$2P_2$	$2M$	$1?S_0$	$1S_1$		$2S_{3/4}$	$4S + 1?S$
ISGS 62P-217 (not figured)	15	$2P_1$	$2P_2$	$2M$	$1?S_0$	$1S_1 + 1?S_1$	$1S_2$	$1S_{3/4}$	$4S$
ISGS 62P-212 (not figured)	14	$2P_1$	$2P_2$	$2M$	$1S_0$	$1S_1$		$4S_{3/4}$	$2S$
Topotype ISGS 62P-210 (Fig. 2.4)	13	$\underline{2P_1}$ ($1P_1^{?s}$, $2P_1^{?d}$)	$\underline{2P_2}$ ($3P_2^{?s}$, $P_2^{?d}$)	$\underline{1M}$ ($5M^d$)		$\underline{1S_1}$ ($7S_1^d$)		$\underline{1S_{3/4}}$ ($12S_{3/4}$)	$\underline{6S}$ ($6S$, $8S$, $9S$, $10S$, $11S$, $13S$)
ISGS 62P-218 (Fig. 2.5)	13	$\underline{2P_1}$ ($1P_1$, $3P_1$)	$\underline{2P_2}$ ($2P_2$, $6P_2$)	$\underline{2M}$ ($4M^s$, $13M^d$)		$\underline{2S_1}$ ($5S_1^s$, $11S_1^d$)	$\underline{2S_2}$ ($9?S_2^s$, $10?S_2^d$)	$\underline{3S_{3/4}}$ ($7S_4^s$, $8S_3^s$, $12S_{3/4}^d$)	
ISGS 62P-211* (not figured)	11	$2P_1$	$2P_2$	$1M + 1?M$				$1S_{3/4}$	$4S$

Montana (UM), Missoula, Montana, USA; U.S. Geological Survey (USGS), Reston, Virginia, USA; U.S. National Museum (USNM), Washington, D.C., USA.

Systematic paleontology

Phylum Chordata Bateson, 1886
 Class Conodontata Pander, 1856
 Order Ozarkodinida Dzik, 1976
 Suborder Ozarkodinina Dzik, 1976
 Superfamily Polygnathacea Bassler, 1925
 Genus *Lochriea* Scott, 1942

- 1941 *Spathognathodus* Branson and Mehl; Branson and Mehl, 1941a, p. 172 [nomen nudum].
 1941 *Spathognathodus* Branson and Mehl; Branson and Mehl, 1941b, p. 98 [partim].
 1942 *Lochriea* Scott, p. 298.
 1953 *Gnathodus* Pander, 1856; Hass, p. 78 [partim].
 1970 *Paragnathodus* Meischner, p. 1173 [nomen nudum].
 non 1973 *Lochriea* Scott, 1942; Melton and Scott, p. 58.
 non 1973 *Lochriea* Scott, 1942; Scott, p. 94.
 1975 *Paragnathodus* Higgins, p. 70.
 1976 *Lochriea* Scott, 1942; Norby, p. 139.
 ?1997 *Neolochriea* Mizuno, p. 253.

Type species.—*Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b).

Diagnosis.—A conodont genus bearing a typical 15-element ozarkodinid feeding apparatus that contains sinistral and dextral pairs of P₁, P₂, M, S₁, S₂, S₃, and S₄ elements, and an unpaired S₀ element. P₁ elements are carminiscaphate and possess a large subcircular, subquadrate, lanceolate or lachrymiform posterior basal cavity below a platform surface that is unornamented, or is ornamented with a few nodes, rows of nodes, or lateral ridges, and a free blade lacking a prominent anterior crest. P₂ elements are angulate, typically with discrete denticles. M elements are makellate, with large cusps and arched posterior processes, typically with discrete denticles decreasing in height distally. S₀ elements are alate. S_{1–4} elements are bipennate with short to medium length anterior processes of three different styles.

Etymology.—Although Scott (1942) did not provide his source or derivation for the genus name *Lochriea*, and did not designate or identify the gender of *Lochriea*, he was almost certainly honoring Elizabeth Lochrie, a highly regarded Montanan artist who painted portraits of Native Americans and their environments, and who drew the illustrations Scott had used eight years before (Scott, 1934, p. 449). We here specify that the genus *Lochriea* be considered a feminine genus. Norby (1976), Mapes and Rexroad (1986), and Sweet (1988), following Branson and Mehl (1941b), used the masculine ending, *-us*, when referring to the *Lochriea* species *L. commutata*. We here apply the feminine ending, *-a*, for all references to the type species of *Lochriea*, *L. commutata*, except in synonymies where we cite earlier work and where

others have ended the species name with an *-a* or *-us* suffix. However, where the original generic name used was masculine, we use the suffix *-us*, such as in *Gnathodus commutatus*.

Procedural notes.—Our generic synonymy (above) is selective and traces the generic assignments of the type species of *Lochriea* from its original description by Branson and Mehl (1941b), until Norby (1976) recognized and acted on the priority of *Lochriea*.

Remarks.—Our diagnosis has been modified from Atakul-Özdemir et al. (2012), it in turn having been modified from Norby (1976).

Atakul-Özdemir et al. (2012, p. 1287) reported that P₁ elements of *Lochriea* species lack a prominent anterior crest, an observation with which we concur; however, we are unable to support or refute their opinion that M elements of *Lochriea* species lack an adaxial bulge at the base of their cusps and possess a basal cavity that is restricted to their cusps.

Sweet (1988, p. 112) observed that “if future studies demonstrate that *Lochriea* and *Vogelgnathus* represent a lineage separate from the Spathognathodontidae and Gnathodontidae, it will probably be desirable to create and name a new family for them,” but recommended that this not be done until the relationships of *Diplognathodus* Kozur and Merrill in Kozur, 1975 and related genera belonging to the Sweetognathidae were considered. The relationship of the various genera in the Sweetognathidae (see Sweet, 1988, p. 188) to one another has not, to our knowledge, yet been clarified, and although we agree about the desirability of establishing a new family that would include *Lochriea*, we, like Donoghue et al. (2008), still regard it premature to do so.

We use the order Ozarkodinida Dzik, 1976, in the sense of Donoghue et al. (2008), who expanded on the systematic concepts for suprageneric classifications based on formal phylogenetic analyses using cladistics, rather than on general perceived relationships.

Even though cladistic analyses are being increasingly used to determine phylogenetic relationships between different conodont genera in an objective, repeatable manner (e.g., Donoghue, 2001; Donoghue et al., 2008; Atakul-Özdemir et al., 2012), Atakul-Özdemir et al. (2012, p. 1287) recovered a clade of *Lochriea* + *Sweetognathus* + *Clydagnathus*, which is an identical grouping recovered by Donoghue et al. (2008). However, Atakul-Özdemir et al. (2012) resolved *Lochriea* in a sister group relationship with (*Sweetognathus* + *Clydagnathus*), whereas Donoghue et al. (2008) consistently resolved a *Lochriea* + *Clydagnathus* clade.

The P₁ elements described by Mizuno (1997) as *Neolochriea hisaharui* and *Neolochriea nagatoensis* are morphologically similar to P₁ elements of species currently assigned to *Lochriea*; those on which *Neolochriea hisayoshii* Mizuno, 1997 and *Neolochriea koikei* Mizuno, 1997 are based are not. This suggests that until the apparatuses of one or more *Neolochriea* species are known and can be compared with those of *Lochriea commutata*, it will remain uncertain whether *Lochriea* spp. and *Neolochriea* spp. are a part of the same lineage in an ancestor-descendent relationship, whether the P₁

elements of species of the two genera are homeomorphs of one another, and whether *Neolochriea* is, in whole or in part, a junior synonym of *Lochriea*.

Lochriea commutata (Branson and Mehl, 1941) (Branson and Mehl, 1941b)
Figures 1–9

- 1941 *Spathognathodus commutatus* Branson and Mehl; Branson and Mehl, 1941a, p. 172, pl. 5, figs. 19–22 (= P₁ elements) [nomen nudum].
- 1941 *Spathognathodus commutatus* Branson and Mehl; Branson and Mehl, 1941b, p. 98, pl. 19, figs. 1–4 (= P₁ elements). These elements were re-illustrated by von Bitter and Norby (1994a, figs. 2.6–2.15, 3.1–3.6, 3.9–3.12), and they selected specimen UM C552-2 as the lectotype (= Fig. 3.7–3.10 of this paper).
- 1942 *Lochriea montanaensis* Scott, p. 298, pl. 37, figs. 1–7, pl. 38, figs. 1–4, 6, 7, 10, 12 are bedding-plane assemblages; p. 298, pl. 39, fig. 1, subhorizontal element, is a dextral S₁ element; a more vertical element may be a dextral S₂ element; “hindeodells,” p. 298, pl. 39, figs. 4, 7 are a pair of sinistral and dextral S_{3/4} elements, respectively; “a pair of prioniods,” p. 298, pl. 39, fig. 9 are two M elements; “hindeodell,” p. 298, pl. 40, fig. 2 is an ?S₁ element; “prioniodells,” p. 298, pl. 40, figs. 9, 10 are P₂ elements; “prioniod,” p. 298, pl. 40, fig. 12 is an M element; “hindeodell,” p. 298, pl. 40, fig. 18 is an S_{3/4} element; “spathognaths,” p. 298, pl. 40, figs. 13, 15, 19 are P₁ elements.
- 1942 *Lochriea bigsnowyensis* Scott, “prioniod,” p. 299, pl. 40, fig. 3 is an M element [partim].
- 1942 unidentified element, Scott, p. 299, pl. 40, fig. 16 is an S₀ element.
- 1958 *Hindeodella montanaensis* (Scott, 1942); Stanley, p. 465, pl. 64, figs. 1–4, 5 are S_{3/4} elements.
- 1958 *Prioniodina montanaensis* (Scott, 1942); Stanley, p. 474, pl. 64, fig. 5 (vertically oriented element) and pl. 65, fig. 1 are both P₂ elements.
- 1969 *Neoprioniodus montanaensis* (Scott, 1942); Rhodes et al., p. 160, pl. 22, figs. 5a–8b are M elements.
- 1970 *Neoprioniodus montanaensis* (Scott, 1942); Marks and Wensink, p. 266, pl. 1, figs. 9, 10 are M elements.
- 1973 *Neoprioniodus montanaensis* (Scott, 1942); Igo, p. 195, pl. 29, fig. 32 are M elements.

Lectotype.—UM C552-2 (von Bitter and Norby, 1994a, figs. 2.6–2.9, 3.9); paralectotypes UM C1139-9, UM C1139-10, and UM C1139-11 (von Bitter and Norby, 1994a, figs. 2.10–2.15, 3.1–3.6, 3.10–3.12).

Diagnosis.—A species of *Lochriea* with a typical 15-element ozarkodinid apparatus containing sinistral and dextral pairs of P₁, P₂, M, S₁, S₂, S₃, and S₄ elements, and an unpaired S₀ element. The carminiscaphate P₁ elements have low platforms that are subcircular to subquadrate in upper view, subrectangular outline in lateral view, are unornamented, and possess cup-shaped basal cavities restricted to the posterior one-half to one-third of the element. The angulate P₂ elements

have slight downward-curving posterior processes and straight anterior processes, both with long typically discrete denticles. The makellate M elements have a large cusp, and an arched and flexed posterior process with typically discrete denticles that decrease in height distally. The alate S₀ elements possess a posterior process of medium length and two short anterolateral processes. The bipennate S₁ and S₂ elements have long posterior processes, and either very short, or medium-length, inwardly flexed anterior processes. The bipennate S₃ and S₄ elements have prominent main cusps, long posterior, and short, inwardly curved, upswept anterior processes.

Description of elements.—

P₁ element (Fig. 3).—The carminiscaphate P₁ element has a subrectangular outline in lateral view and is ~3–5 times as long as high, typically narrowing toward the base to varying degrees at the posterior end giving it a slightly arched appearance. In upper view, the element can be nearly straight, but typically curves toward the inner side with a smooth and unornamented low platform, typically asymmetric and slightly wider on the inner side, occupying the posterior one-third to one-half of the element. The blade typically consists of 15–18 denticles with a noted maximum of 22 and <15 in immature elements; blade may extend slightly beyond posterior tip. Denticles on the anterior free blade are generally fused along most of their length with just the tips exposed, which are sharp edged in immature forms but are more rounded in mature elements. Denticles on the posterior blade (carina) above the basal cavity generally fuse completely along all their length and in some mature elements widen considerably to include microsculpture, this sometimes extending onto the anterior free blade. In lower view, the basal cavity can be semicircular, oval, or subquadrate, tapering sharply on both axial ends, but more so on the posterior end.

P₂ element (Fig. 4).—The angulate P₂ element is straight to nearly straight in oral view, typically thin and laterally compressed. The anterior process is nearly straight to slightly arched upwards in lateral view with a few to a dozen vertical to slightly posteriorly inclined denticles that are typically unfused but can be fused in more mature elements. The slightly to moderately downward-arched posterior process has a few to a dozen typically unfused denticles that recline at increasing angles posteriorly, and on some specimens exhibits a few small denticles interspersed between the larger denticles. The cusp is nearly vertical, slightly larger and higher than the denticles on the two processes. The basal cavity is typically small and elongate with some noticeable lateral flare in some elements.

M element (Fig. 5).—The makellate M element has a large, typically straight to slightly inwardly flexed, laterally compressed, sharp-edged and pointed cusp with a moderately short undenticulated anticusp and an arched, typically inwardly flexed, posterior process of approximately one-half the length of the cusp in inner lateral view. The denticles on the posterior process are typically unfused, begin about one-quarter the length from the cusp tip, abruptly decrease in height and gradually recline distally. The basal cavity is small to moderately large and everted in many mature elements.

S₀ element (Fig. 6).—The alate S₀ element is characterized by a large anterior cusp that is compressed laterally with two

anterolateral processes that branch from sharp anterior costae on each side of the lower third of the cusp. These processes are relatively short, project slightly anteriorly forming an anterior angle of $\sim 145\text{--}180^\circ$ in upper view, diverge widely ($\sim 145^\circ$) aborally in anterior view, and typically recurve slightly to the posterior with typically small denticles that tend to alternate slightly in size. The short to medium-length posterior process is slightly to moderately arched upward and is $\sim 50\text{--}60\%$ of the length of the posterior process of S_{1-4} elements of similar maturities. Denticles on the posterior process gradually recline distally, alternate in size and height, and typically increase in size and height in the distal half. A very small aboral basal pit occurs at the junction of the three processes.

S_1 element (Fig. 7).—The bipennate S_1 element consists of a small cusp, commonly inclined inward with a moderately long anterior process that initially bends outward then inward at $90\text{--}120^\circ$ and slightly downward. This process bears 8–12 denticles that alternate in size and are nearly vertical where the process projects from the cusp, but progressively recline and increase in size toward the upswept distal end. The secondary denticles on the posterior process of S_1 elements may bend slightly inward, a feature observed on some of the specimens from the Bluestone Formation of West Virginia (Fig. 7.18). The moderately long posterior process is slightly to moderately arched in lateral view, bearing an alternating dentition. The basal pit is small and continues as a small basal groove under both processes.

S_2 element (Fig. 8).—The bipennate S_2 element consists of a moderately long, nearly straight to slightly arched posterior process with a typical alternating denticulation with a typical slight upsweep at its distal end. The cusp is subequal or slightly larger than the secondary denticles on either process, and the cusp typically bends inward. The anterior process is relatively short, projects anteriorly, with a very short bend outward, followed by a sharp bend inward, forming an inner angle of 90° or less with the posterior process, and curves slightly downward, typically exhibiting three to four secondary and about four to more tertiary denticles. The basal pit is small and continues as a small basal groove under both processes.

$S_{3/4}$ element (Fig. 9).—The bipennate $S_{3/4}$ element has a large, prominent, pick-like cusp, which gently inclines posteriorly. The short anterior process bears five to eight denticles, the first one to three small denticles are typically situated high on the anterior slope of the cusp followed anteriorly by an increase in denticle size to the upturned distal end, where some are one-third to one-half the height of the cusp. As the denticles increase in height, the anterior process curves smoothly inward until it forms an angle of $\sim 90^\circ$ with the posterior process, and curves upward to a noticeable degree. The bar portion of the anterior process tends to be higher than that of the S_1 and S_2 elements, causing it to have an elongated ovoid cross section. The denticles of the posterior processes alternate in size and are noticeably longer than are those of S_1 and S_2 elements. In lateral view, the posterior process is relatively straight, with gentle arching occurring only near the anterior end of some specimens.

Remarks.—Our specific synonymy (above) is selective and seeks to integrate the single-element taxonomy of Branson and Mehl (1941b) with that based on multielement concepts used

by Scott (1942). Also, because the *Lochriea commutata* P_1 element, unlike the remaining elements of the *Lochriea commutata* apparatus, is both well known from the literature and uncontroversial, we have avoided providing a long, exhaustive list of previous identifications and illustrations.

We have applied the morphological descriptors of Sweet (1981, 1988) to describe the shape, orientation, and morphology of individual elements in the feeding apparatus of *L. commutata*, and the biological terminology of Purnell et al. (2000) to describe the orientation and position of elements within the feeding apparatus of *L. commutata* (Fig. 12).

Stanley (1958) was apparently the first to apply nomenclatural priority of a Carboniferous conodont species name, based on conodont elements in bedding-plane assemblages, to subsequently studied discrete Carboniferous conodonts. He did this when he identified $S_{3/4}$ elements as *Hindeodella montanaensis*, and P_2 elements as *Prioniodina montanaensis*, designating lectotypes for these two species from the illustrations of Scott (1942). Rhodes et al. (1969, p. 123, 160, pl. 22, figs. 5–8, pl. 28, figs. 21, 26), and subsequently Marks and Wensink (1970, p. 266, pl. 1, figs. 9, 10) and Igo (1973, p. 195, pl. 29, fig. 32), identified particular S and M elements as the species *montanaensis*. Remarkably, none of these authors applied this taxonomic procedure to the *Lochriea montanaensis* P_1 element that was abundant as discrete elements in their collections. For example, although Stanley (1958, p. 465), synonymized *Spathognathodus commutatus* Branson and Mehl, 1941 (Branson and Mehl, 1941b) with, and apparently incorrectly assigned priority to, the later-named *Gnathodus inornatus* Hass, 1953, he did not recognize these P_1 elements as *montanaensis*, which is something he was able to do for the P_2 and $S_{3/4}$ elements he regarded as identical to those present in the bedding-plane assemblages of *L. montanaensis* Scott, 1942. Similarly, although Rhodes et al. (1969, p. 95, 96), Marks and Wensink (1970, p. 258), and Igo (1973, p. 193) recognized and acknowledged that particular discrete M elements were identical to those in the bedding-plane assemblages of *Lochriea montanaensis* Scott, 1942, they continued to identify abundant P_1 elements as *Gnathodus commutatus*.

The final remaining step in this evolving, and now accepted, taxonomic procedure was to apply a Carboniferous conodont genus name having priority, but based on bedding-plane assemblages, to discrete Carboniferous conodonts. Varker and Sevastopulo (1985, p. 183) apparently took this step when they reported *Lochriea singularis* (Hass), an M element, from the *Michelinia grandis* beds of the *Cloghergnathus* Zone at Ravenstonedale, Cumbria, England.

The lower surface of some elements, primarily of the M and S elements, of *Lochriea commutata* have a moderately strong to strong tendency toward eversion of the basal cavity, resulting in a well-developed attachment scar (see von Bitter and Merrill, 1983, text-fig. 1A, 1B, for a representation of how this feature develops in the ontogeny of this and other conodont species). An everted basal cavity is well developed and common on the basal surface of M elements (Fig. 5.16–5.18, 5.20), is present in some mature S_0 elements (Fig. 6.11), and is common in $S_{3/4}$ elements (Fig. 9.15–9.21); the basal surfaces of P_1 , P_2 , S_1 , and S_2 elements show less of a tendency toward eversion. The denticulation of S elements is characterized by the

alternation of prominent long, single denticles that are separated by two or three denticles of reduced length. Denticles of elements other than the P₁ elements exhibit striae 2–5 µm apart; these are somewhat finer on the cusp of M elements (Norby, 1976).

Discussion

P₁ element (Fig. 3).—Having previously (von Bitter and Norby, 1994a, b) correlated the changes in the width of carinal nodes and their microsculpture fields with an increase in element size, we agree with Rhodes et al. (1969, p. 96) and Metcalfe (1981, p. 21) that the morphology of the *Lochriea commutata* P₁ element is variable. The length to height ratio typically increases with ontogeny by becoming more elongated (greater length to height), as noted in the lectotype and paralectotypes of the species (von Bitter and Norby, 1994a, figs. 2.6–2.15, 3.1–3.6), but particularly for specimens from the Heath and Tyler formations of Montana (von Bitter and Norby, 1994a, figs. 6, 7), and reaches a maximum length to height ratio in specimens from the Heath Formation (von Bitter and Norby, 1994a, fig. 7).

Blade denticulation of P₁ elements is also variable, with the lectotypes and paralectotypes of the species, for example, not being particularly denticulate (von Bitter and Norby, 1994a, figs. 2, 3), which Branson and Mehl (1941b, p. 98) described as having a tendency “to fuse.” Microsculpture is absent on the denticles of these specimens, with the upper denticle surface being covered by secondary crystal overgrowths (von Bitter and Norby, 1994a, fig. 3.9–3.12). We conclude that *Lochriea commutata* P₁ elements vary from being relatively short with stubby, commonly fused blade denticles and carinal nodes to more elongate with better-defined blade denticles and carinal nodes (Fig. 3).

Variation in P₁ element morphology has been the most frequently applied criterion for recognizing and defining conodont species. Among *Lochriea* species with unornamented P₁ elements, recognition of such variation has led to the definition of species such as *Spathognathodus pellaensis* Youngquist and Miller, 1949, *Gnathodus inornatus* Hass, 1953, *G. commutatus nagatoensis* Igo and Koike, 1965 (the latter included by Mizuno, 1997, in *Neolochriea*), *G. scotiaensis* Globensky, 1967, and *G. simplicatus* Rhodes et al., 1969, the latter species recently placed in *Pseudognathodus* by Sanz-López et al., 2018. Confirmation that these species with unornamented P₁ elements are valid species related, or unrelated, to *Lochriea commutata* must await monographic and biometric study. Increasingly, it will also be necessary to determine the element composition of their apparatuses to confirm or refute these relationships.

P₂ element (Fig. 4).—We recognize three main morphotypes of *Lochriea commutata* P₂ elements in North America, two of which appear to intergrade, based on the degree of arching of the posterior process, on the degree of denticle separation or fusion, and on the overall length/height ratio. The first, the *montanaensis* morphotype, is the classic one illustrated by Scott (1942, pl. 40, figs. 9, 10), and is often found in bedding-plane assemblages from Montana (Fig. 4.1, 4.2, 4.5, 4.7, 4.19, 4.22). It is recognized as possessing a strong

upward-arching posterior process and generally distinct denticle separation, particularly on the posterior process.

Some *montanaensis* morphotype P₂ elements illustrated in the literature are *Prioniodina montanaensis* (Scott, 1942), Stanley, 1958, p. 474, pl. 64, fig. 5 (lower left specimen), pl. 65, fig. 1; ?*Prioniodina* sp. A Stanley, 1958, p. 474, pl. 65, fig. 3; *Prioniodina* sp. B Stanley, 1958, p. 474, pl. 65, fig. 7; ?*Prioniodina* sp. C Stanley, 1958, p. 474, pl. 65, fig. 2; and ?*Ozarkodina deflecta* Stanley, 1958, p. 472, pl. 65, figs. 4, 5.

The second, the *recta* morphotype, is characterized by *Ozarkodina recta* of Rexroad, (1957, pl. 2, figs. 5, 6) and is recognized by its less-pronounced arching of the posterior process and denticles that tend to be somewhat shorter and fused along part of their length (Fig. ?4.3, 4.21, 4.23). Intergradations between the *montanaensis* and *recta* morphotypes are shown in Figure 4.18 and 4.20. Those shown in Figure 4.4 and 4.6 do not fit either of the two end-member morphotypes precisely; however, the specimen illustrated in Figure 4.4 is probably closer to the *montanaensis* morphotype. Both examples show some downward arching of the tip of the anterior process, which is seen in only a few examples of the *recta* morphotype (e.g., Fig. 4.22).

Some *recta* morphotype P₂ elements illustrated in the literature are *Ozarkodina recta* Rexroad, 1957, p. 36, pl. 2, figs. 5, 6; ? Rexroad and Furnish, 1964, p. 674, pl. 111, fig. 8; Thompson and Goebel, 1969, p. 41, pl. 3, fig. 22; and *Ozarkodina* cf. *O. recta* Rexroad, Dunn, 1970, p. 338, pl. 62, figs. 25, 26.

The Bluestone morphotype (Fig. 4.9–4.17), based on P₂ elements from the Bluestone Formation of West Virginia, is recognized as a third morphotype; it is similar to the *montanaensis* morphotype, but the length/height ratios differentiate the Bluestone and *montanaensis* morphotypes. The Bluestone morphotype P₂ elements show shorter anterior and posterior processes that possess exceptionally long, non-fused, comb-like denticles whose lengths are commonly two to three times that of the supporting process bar. Further study of the Bluestone morphotype may lead to the recognition and definition of a new subspecies of *Lochriea commutata*. Bluestone morphotype P₂ elements have not been described previously and are illustrated in Figure 4.9–4.17.

The fourth morphotype, the *subaequalis* morphotype, is based on *Subbryantodus subaequalis* of Higgins (1961, pl. 12, fig. 15), and is likely the *Lochriea commutata* P₂ element most common in Europe. It shows similarities to both the *montanaensis* and *recta* morphotypes, exhibits some arching of the posterior process, and often shows alternation of slightly smaller denticles with larger denticles on the anterior process. Although we did not recover or recognize the *subaequalis* morphotype in North American collections, Scott (1942, pl. 40, figs. 4, 5) illustrated examples that are similar.

Some *subaequalis* morphotype P₂ elements in the literature are *Subbryantodus subaequalis* Higgins, 1961, p. 218, pl. 12, fig. 15, text-fig. 6; Higgins and Bouckaert, 1968, p. 47, pl. 3, figs. 1, 2; Higgins, 1975, p. 74, pl. 5, fig. 17; Metcalfe, 1981, pl. 19, fig. 17; *Prioniodina subaequalis* (Higgins), Rhodes et al., 1969, p. 198, pl. 28, figs. 1a–4; *Ozarkodina subaequalis* (Higgins), Marks and Wensink, 1970, p. 267, pl. 1, fig. 13 only; ?*Subbryantodus stipans* Rexroad, 1957, Higgins, 1961, p. 219, pl. 12, fig. 14, text-fig. 6; Higgins, 1962a, p. 13, pl. 1, fig. 9, text-fig. 2; ?*Prioniodina stipans* (Rexroad), Rhodes

et al., 1969, p. 198, pl. 28, figs. 7a–10c; *Ozarkodina plana* (Huddle), Reynolds, 1970, p. 2, pl. 2, fig. 12; *Lochriea commutata* Pb element, Stone, 1991, p. 34, pl. 4, fig. 14; *Lochriea* sp. Pb element, Varker, 1994, pl. 4, figs. 11, 12.

Most Montana P₂ elements are of the *montanaensis* morphotype, although some mature elements from the Tyler Formation of Montana that tend to be larger and have more completely fused denticles are of the *recta* morphotype. Most Illinois P₂ elements are of the *recta* morphotype; however, they are generally smaller than Montana specimens, and conversely, a few Illinois P₂ elements are of the *montanaensis* morphotype. The Bluestone morphotype has been recovered from only a single locality in West Virginia and presently appears to be restricted to eastern North America.

Although all elements exhibit breakage, many more elements, particularly the P₁, M, and S_{3/4} elements, can be recognized from fragmented or smaller remains than can the P₂ elements. The thin, blade-like nature of the anterior and posterior processes of P₂ morphotypes and the fragility of their discrete denticles lead to breakage, which makes it difficult to identify discrete P₂ elements.

The co-occurrence of *L. commutata* P₁ elements and P₂ *recta* morphotypes in the Renault and Ridenhower formations of Illinois (Rexroad, 1957, table 1), as well as in our own collections from the Ridenhower Formation of Illinois, suggests that they were part of the same apparatus. However, the cluster analysis applied by Horowitz and Rexroad (1982, p. 966, text-fig. 3) to Chesterian conodont collections from the Beech Creek, Haney, and Glen Dean formations of Indiana failed to group the *recta* element with the P₁, M, and S elements they hypothesized to be parts of the *Lochriea commutata* apparatus. The authors nevertheless included the *recta* element in the statistical reconstruction of the species (text-fig. 10), attributing the failure of the clustering procedure to low element occurrences and difficulties in identifying broken elements, also noting that current sorting and breakage also affects the presence and abundance of conodonts. Subsequently, Rexroad and Horowitz (1990, p. 509) did include *Ozarkodina recta* and *O. subaequalis* in their extensive synonymy of the Pb (= P₂) element of *Lochriea commutata*.

M element (Fig. 5).—This large pick-shaped element is, along with the P₁ element and perhaps the S_{3/4} elements, the most distinctive element of the *L. commutata* apparatus. Variation in this element includes differences in denticle spacing, the angle of the posterior bar to the apical denticle, and the length of the anticusp. Many mature specimens from the Heath and Tyler formations of Montana and the Bluestone Formation of West Virginia show well-developed attachment scars (Fig. 5.7, 5.8, 5.12, 5.14), whereas this feature is less well developed in immature specimens, such as in those from the Ridenhower Formation of Illinois (Fig. 5.21, 5.22). Examination of the two associated M elements illustrated by Scott (1942, p. 298, pl. 39, fig. 9) show them to be outer lateral views of sinistral and dextral M elements of similar maturity. This is probably a fortuitous association because no other elements occur in the vicinity of these two elements, and we know of no other *L. commutata* M elements in such direct association with each other.

Some M elements of *Lochriea commutata*, or of related *Lochriea* spp., illustrated in the literature are *Prioniodus*

singularis Hass, 1953, p. 88, pl. 16, fig. 4; *Prioniodus roundyi* var. *dividen* Elias, 1956, p. 110, pl. 2, figs. 39–41; *Prioniodus* cf. *P. singularis*, Elias, 1956, p. 112, pl. 2, fig. 45; *Prioniodus roundyi* var. *parviden* Elias, 1956, p. 112, pl. 2, figs. 42, 43; *Prioniodina alatoidea* (Cooper), Bischoff, 1957, p. 45, pl. 5, figs. 33, 34, 36; *Prioniodus* sp. A Ziegler in Flügel and Ziegler, 1957, p. 50, pl. 4, fig. 3; *Neoprioniodus singularis* (Hass), Stanley, 1958, p. 471, pl. 66, figs. 2, 3; Higgins, 1961, pl. 11, fig. 5; Higgins, 1962a, pl. 1, fig. 8; Higgins, 1962b, p. 68, pl. 3, fig. 11; Rexroad and Furnish, 1964, p. 674, pl. 111, fig. 32 (listed as fig. 33 in text); Higgins and Bouckaert, 1968, p. 45, pl. 1, fig. 8; Webster, 1969, p. 40, pl. 7, fig. 14; Dunn, 1970, p. 337, pl. 64, figs. 32, 33; Thompson, 1972, p. 37, pl. 1, figs. 21, 22; Lane and Straka, 1974, fig. 34.1; Higgins, 1975, p. 68, pl. 3, fig. 11 (not Higgins and Varker, 1982, pl. 19, fig. 15); Metcalfe, 1981, pl. 18, figs. 1–3; *Neoprioniodus* sp. A Stanley, 1958, p. 472, pl. 66, figs. 4, 5; *?Neoprioniodus miser* Elias, 1959, p. 154, pl. 2, figs. 23, 24; Elias, 1966, p. 26, pl. 2, figs. 23, 24; *Neoprioniodus* aff. *N. alatoideus* Elias, 1959, p. 155, pl. 2, fig. 3 (only); Elias, 1966, p. 27, pl. 2, fig. 3 (only); *?Neoprioniodus singularis* (Hass), Globensky, 1967, p. 444, pl. 55, figs. 23, 24; Koike, 1967, p. 307, pl. 4, fig. 30; *Neoprioniodus montanaensis* (Scott), Rhodes et al., 1969, p. 160, pl. 22, figs. 5a–8b; Marks and Wensink, 1970, p. 266, pl. 1, figs. 9, 10; Igo, 1973, p. 195, pl. 29, fig. 32; *Lochriea commutata* M element, Stone, 1991, p. 34, pl. 4, fig. 13; *Lochriea* sp. element, Varker, 1994, pl. 1, fig. 5, 6 (both clusters contain the characteristic *Lochriea commutata* M element); *Lochriea* sp. M element, Varker, 1994, pl. 4, figs. 13, 14.

S₀ element (Fig. 6).—The S₀ element of *L. commutata* is rare because it is only one of 15 elements in the apparatus and because of its susceptibility to breakage, being exceeded in rarity only by the S₁ and S₂ elements. This alate element is, like most elements of this general morphology, particularly susceptible to breakage when compressed laterally, the result being that its two anterolateral processes, and or its posterior process, are generally broken. The posterior process (Fig. 6.3–6.5, 6.14) has prominent terminating denticles at its posterior end, making it unlikely to be confused with those of any of the other S elements. Although an uncommon feature, a few specimens exhibit an everted lower surface (Fig. 6.11).

Although Scott (1942) did not recognize an S₀ element to have been a part of the *L. commutata* apparatus, he illustrated (Scott, 1942, pl. 40, fig. 16) and recognized (p. 299 in pl. 40 explanation) an S₀ element as “the only specimen of its kind found in the Heath shales.” Some S₀ elements of *Lochriea commutata*, or of related *Lochriea* spp., illustrated in the literature are *Hibbardella pennata* Higgins, 1961, p. 213, pl. 12, figs. 5, 6; Reynolds, 1970, p. 2, pl. 2, figs. 8, 9; Higgins, 1975, p. 36, pl. 1, fig. 6 (only); Metcalfe, 1981, pl. 14, figs. 1a, 1b, 4a, 4b; Riley et al., 1987, pl. 2, fig. 15; *?Higgins and Bouckaert, 1968, p. 36, pl. 1, fig. 10; ?Hibbardella (Hibbardella) parva* Rhodes et al., 1969, p. 114, pl. 25, fig. 21a, 21b.

Other than Norby (1976, p. 157, pl. 11, figs. 15a, 15b, 17a–18), who described this as the A₃ element of *L. commutatus*, only Mapes and Rexroad (1986, p. 115, pl. 1, fig. 21) and Rexroad and Horowitz (1990, p. 510, pl. 2, fig. 25) referred to this element, describing it as the Sa element of this species. Varker

(1994, pl. 4, fig. 7) referred a well-preserved S_0 element to *Lochriea* sp., which we would include in *L. commutata*.

This element can be confused with S_0 elements belonging to species of other genera, particularly those of *Gnathodus*. S_0 elements of *G. bilineatus* have a much more acute angle, $<60^\circ$, between the lower edges of the two anterolateral processes (e.g., Varker, 1994, pl. 3, fig. 8), whereas that same angle is 145° or greater in *Lochriea commutata* S_0 elements (cf., Varker, 1994, pl. 4, fig. 7).

S_1 element (Fig. 7).—Scott (1942) illustrated an S_1 element as a “hindeodell” element of *Lochriea montanaensis* (Scott, 1942, pl. 39, fig. 1, subhorizontal element). The S_1 element has a characteristic scythe-shaped or shepherd’s crook morphology, with an angle of $\sim 70^\circ$ (Fig. 7.8–7.10, 7.13–7.17) to 90° (Fig. 7.3, 7.12, 7.18) between the anterior and posterior processes. The S_1 element (Fig. 7.1, 7.2) was described and figured by Norby (1976, text-fig. 21, pl. 12, fig. 5c, 5d) as the *Lochriea commutatus* A_{1c} element, and by Purnell and Donoghue (1998, text-fig. 11A) as the S_{b1} element of *Lochriea* sp.

The juncture between the anterior and the posterior processes of *Lochriea commutata* S_1 elements is broadly curved and expanded laterally (Fig. 7), resulting in the characteristic shepherd’s crook shape of their anterior ends. Discrete S_1 elements are generally broken (e.g., those from bleach-processed residues from the Heath Formation), and are reported and illustrated only infrequently. Similarly, S_1 elements are rarely identified in bedding-plane assemblages, and the anterior ends needed to identify them are generally preserved only as short broken stubs, (e.g., in bedding-plane assemblages from Montana; Fig. 7.1–7.4). The best-preserved, complete, discrete S_1 elements (Fig. 7.9–7.18) and S_1 element pairs (Fig. 7.5–7.8) were those recovered with, or in, fused clusters from West Virginia. One remarkable S_1 element pair (Fig. 7.7) shows the anterior process of the dextral S_1 element closely interlocked with the anterior process of the sinistral S_1 element, and preserving the two elements in a tight embrace with their anterior processes facing one another (Figs. 4.8, 5.4, 7.5–7.7), and in another (Fig. 7.5, 7.6) the element embrace not being as tight (i.e., the elements having moved relative to one another). The interlocked S_1 elements of *Lochriea commutata* (Figs. 4.8, 5.4, 7.5–7.7), like those illustrated by Varker (1994, pl. 1.4) in a fused cluster of *Gnathodus bilineatus* from England, are positioned over the posterior ends of the long posterior process of the central S_0 element (Figs. 4.8, 5.5, 7.7), S_1^d and S_2^d are preserved farther posteriorly than the other S elements. Because S elements were located and functioned at the anterior end of the feeding apparatus (Aldridge et al., 1987; Purnell and Donoghue, 1998, text-fig. 1e) (Fig. 12), and are not known to have functioned in apposition to one another, both the position and the interlocking nature of the S_1 elements in fused clusters of both species are presently best accounted for by post-mortem contraction.

Ramiform elements with a scythe or shepherd’s crook shape, similar to those of *Lochriea commutata* S_1 elements, have been illustrated in the Carboniferous conodont literature. These include upper views of *Hindeodina uncata* Hass, 1959, p. 383, pl. 47, fig. 6; *Hindeodella uncata* (Hass), Metcalfe, 1981, pl. 15, ?fig. 2; *Hindeodella brevis* Branson and Mehl,

Higgins, 1961, pl. 10, fig. 14; and *Hindeodella croka* Rhodes et al., 1969, p. 121, pl. 28, figs. 15, 17. *Hindeodina uncata* occurs in early Carboniferous strata and is probably the S_1 element of a species of *Gnathodus* or of a related gnathodontid, a likelihood Varker (1994, p. 309) recognized when he identified this element, *Hindeodella uncata* (Hass), as the *Gnathodus bilineatus* Sd element. Higgins (1975, p. 44, pl. 4, figs. 1–3) illustrated upper and lateral views of *Hindeodella uncata* that possesses a gently downward-arching anterior process.

S_1 elements of gnathodontids, particularly those of *Gnathodus bilineatus*, as illustrated in Norby, 1976, pl. 7, figs. 6, 8, 9, 11 (A_{1c} element), Aldridge et al., 1987, fig. 4.1 (Sd element), polygnathacean apparatuses and reconstructions, Aldridge et al., 1987, fig. 4.7–4.12 (unlabeled Sd elements), Varker, 1994, pl. 1, figs. 3, 4, 7, pl. 2, fig. 1 in fused clusters of *G. bilineatus* and in pl. 3, figs. 13, 15 as discrete *G. bilineatus* Sd elements, and of *Streptognathodus/Ildiognathodus* von Bitter, 1972, pl. 11, fig. 4a–d (*Hindeodella parva*), are similar to *Lochriea commutata* S_1 elements; however, they can generally be differentiated from *Lochriea* spp. S_1 elements by the characteristic sharp downturn, or anticusp-like extension, of the distal end of their anterior process, their more robust denticles, and the robustness and arching of their posterior process.

S_2 element (Fig. 8).—The S_2 element is approximately the same length as an S_1 element of similar maturity, and slightly shorter than $S_{3/4}$ elements. Like S_1 elements, the S_2 element is very rarely preserved intact, and has been difficult to recognize and characterize in bedding-plane assemblages from the Heath and Tyler formations (Fig. 8.1–8.4). The exceptionally preserved specimens associated with fused clusters in the Bluestone Formation of West Virginia (Fig. 8.5–8.12) have provided the basis for much of the foregoing description.

Because S_2 elements lack strong morphological features and tend to break easily during compaction, it has been difficult to recognize them among the thousands of pieces of disjunct S elements recovered from Montana. Similarly, we have been able to identify and illustrate only a few S_2 elements in bedding-plane assemblages of *Lochriea commutata*, generally only with a question mark (Fig. 8.4; Table 1). As with the other exceptionally preserved S elements in the Bluestone Formation of West Virginia, the S_2 elements recovered with fused clusters (Fig. 8.5–8.12) have provided the basis for most of our understanding and description of S_2 elements.

Scott (1942, pl. 39, fig. 1, nearly vertical element) illustrated a possible S_2^d element that crosses an S_1^d element and is the only such element that we identified among his illustrated material of *Lochriea montanaensis*. Higgins (1975, p. 43, pl. 6, figs. 1–3, 5) named *Hindeodella sinuosa* on the basis of elements from Great Britain that are morphologically similar to *Lochriea commutata* S_2 elements (Fig. 8). *Hindeodella sinuosa* Higgins has the same range as P_1 elements of *Lochriea commutata* and other *Lochriea* species illustrated by Higgins (1975, p. 70–72) as species of *Paragnathodus*: *P. commutatus* (pl. 7, figs. 7–9, 11, 13, 16, 20, 21), *P. cruciformis* (pl. 7, fig. 10), *P. mononodosus* (pl. 7, fig. 14), and *P. nodosus* (pl. 7, figs. 12, 15, 17–19, 22, 23). More recently, Varker (1994, p. 310, pl. 1, fig. 6) illustrated *Hindeodella sinuosa* in a fused cluster of *Lochriea* sp., and two discrete S elements, as the “probable”

Sb elements of *Lochriea* sp. (Varker, 1994, p. 310, pl. 4, figs. 16, 18), here regarded as S₂ elements.

S_{3/4} element (Fig. 9).—The S_{3/4} element is the most commonly recognized S element of the *Lochriea commutata* apparatus, and is abundant in collections of discrete elements, bedding-plane assemblages, and fused clusters of the species. This abundance is primarily due to the relative robustness of the anterior process, which is a structure that does not appear to break as easily as that of S₁ and S₂ elements, making it easier to recognize the element. S_{3/4} elements are the only elements in the *L. commutata* apparatus that we are unable to distinguish from one another on purely morphological grounds (i.e., we are able to differentiate them only by their position within the apparatus). Thus, the S elements in the dextral nested S_{3/4}^d element pair (Figs. 8.12, 9.11) and the sinistral S_{3/4}^s element pair (Fig. 9.1, 9.5) exhibit no morphologic differences that presently allow us to distinguish them from one another in discrete element collections. The S_{3/4} elements are among the three most morphologically diagnostic elements of the species. One prominent feature is the large cusp with its anterior process, which is about one-third the height of the cusp and two or three times the height of the posterior process. The anterior denticles increase in height anteriorly giving the process an upswept appearance, which is an atypical feature in ozarkodinid S_{3/4} elements.

Some examples of S_{3/4} elements of *Lochriea commutata*, or of related *Lochriea* species, illustrated in the literature are *Hindeodella bigeniculata* Elias, 1956, p. 106, pl. 1, figs. 20, 21, (non pl. 1, fig. 16), line drawings only; *Hindeodella mehli* Elias, 1956, p. 108, pl. 1, fig. 24 (?figs. 22, 23), line drawings only; Metcalfe, 1981, p. 29, pl. 15, fig. 3; *Hindeodella germana* Holmes, 1928; Bischoff, 1957, p. 27, pl. 6, fig. 32 (non pl. 6, fig. 34); Higgins, 1961, pl. 10, fig. 12 (?fig. 13); Higgins and Bouckaert, 1968, p. 36, pl. 1, fig. 12; Higgins, 1975, p. 38, pl. 5, fig. 6; *Hindeodella montanaensis* (Scott), Stanley, 1958, p. 465, pl. 64, figs. 1–4, 5 (upper specimen); Rhodes et al., 1969, p. 123, pl. 28, figs. 21, 26; *Lochriea commutata* Sc element, Rexroad and Horowitz, 1990, p. 510, pl. 2, fig. 24; *Lochriea commutata* Sc₁ element, Stone, 1991, p. 34, pl. 4, fig. 12; *Lochriea* sp. Sc element, Varker, 1994, p. 310, pl. 4, figs. 15, 17; possibly present as an S element in a fused cluster identified as *Lochriea* sp. (Varker, 1994, pl. 1, fig. 5).

Acknowledgments

We thank R. Ethington (University of Missouri), D. Blake (University of Illinois at Urbana-Champaign), and J. Carter (Carnegie Museum of Natural History) for permitting us to study type and other conodont collections in their care; S.-W. Norby (University of Illinois at Urbana-Champaign) and G. Gomulka (University of Toronto) for scanning electron microscopy; K. David and the late J. Burke (Royal Ontario Museum) for much capable assistance during the preparation of early versions of this paper; H. Choong (formerly Royal Ontario Museum, now Royal British Columbia Museum), D. Byers, M. Knapp, and S. Krusemark (Illinois State Geological Survey) for providing vital technical expertise during the later stages of preparing figures and tables and for editing the manuscript prior to

submission; J. Repetski (United States Geological Survey) for reviewing the manuscript; D. Korn (Museum für Naturkunde Berlin) for sharing information and updates on the German Carboniferous; the Palaeontological Association for its permission to reproduce plate 2 and text-figure 11 of Purnell and Donoghue (1998) as Figures 13 and 14, respectively, and M. Purnell (Leicester University) for supplying originals of these illustrations, and subsequently providing, and allowing us to publish, an updated version of their text-figure 11A, as Fig. 14.1.

We thank Journal of Paleontology Managing Editor J. Kastigar for her encouragement and helpful technical advice, Journal of Paleontology Associate Editor S. Leslie (James Madison University), and reviewers M. Purnell and J. Over (State University of New York at Geneseo) for their helpful comments and suggestions. The reviewers' comments, particularly those of M. Purnell, led to a stronger paper, and are very much appreciated; any shortcomings that remain are, of course, ours.

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Appendix: Locality Data

Localities in Montana (1–3) and Oklahoma (4, 5), USA, correspond to localities 1–5 in von Bitter and Norby (1994a). Locality 8 in Mercer County, West Virginia, USA, is newly described here, but was sampled by Weems and Windolph (1986) for fossil fish. Locality 9, drill hole SB-1 at Stewiacke, Colchester County, Nova Scotia, Canada, may be found in Utting (1980) and in von Bitter et al. (2007). Locality 10, Am Schälk, near Letmathe, Germany, is more specific than was provided for localities 1A and 1B in von Bitter and Norby (1994b).

Locality 1 (Montana).—Heath Formation, sec. 27, T14N R20E, Fergus County (Loco Ridge 7.5' Quadrangle), Montana, USA. Carnegie Museum no. 33965 was collected by Richard Lund at an unknown level in the formation at this locality. Scott (1942, 1969) and Easton (1962) probably sampled the Heath Formation at this locality as USGS locality 13366.

Locality 2 (Montana).—Heath Formation, NE SW SW sec. 26, T14N R19E, Fergus County (Heath 7.5' Quadrangle), Montana, USA; ~8.3 km S of Heath on E side of road. Red Hill Road section of Norby (1976). Samples H-A-1-1 and H-A-2-2, plus subsample H-A-2-7-1, were collected by Norby (1976) in brownish black fissile shale at two exposures, ~91 m (~100 yards) apart, from the northern outcrop and southern outcrop, respectively, of the upper Heath Formation. This is likely the topotype locality of *Lochriea montanaensis* Scott, 1942.

Locality 3 (Montana).—Tyler Formation, Stonehouse Canyon Member on line between SE NW SE sec. 23 and SW NE SE sec. 23, T14N R20E, Fergus County (Loco Ridge 7.5' Quadrangle), Montana, USA. Locality consists of two short roadcut exposures, each ~2 m (6.5 ft) thick and ~5 m (15 ft) apart. H-B-1-A was a bulk sample representing the entire 15 cm (6 in.) bed of brownish-black fissile shale at the top of the exposure. Sample H-B-1-B was a bulk sample of the entire 50 cm (20 in.) thick bed of fissile black shale at the top of the exposure; sample H-B-1-B-1 was taken in the lowest 10 cm (4 in.) of the previous 50 cm (20 in.) thick sampling unit. Tyler Creek section of Norby (1976) and Norby and Rexroad (1985).

Locality 4 (Oklahoma).—Hindsville Formation in SW SE SE sec. 22, T25N R21E, Craig County (Vinita NE 7.5'

Quadrangle), Oklahoma, USA; 13.2 km SW of Afton in road ditch on the N side of combined U.S. Highway 60, 66, and 69. Only a few cm of exposed limestone of the upper Hindsville Formation were sampled by Norby in 1987; von Bitter and Norby (1994a) listed this as sample 4, the only sample taken at field stop 3 in 1987. Corresponds to locality 1299 of Branson and Mehl (1941b) and is the type locality for *Lochriea commutata*. See Branson et al. (1965) for the identification of the Hindsville Formation at this locality.

Locality 5 (Oklahoma).—Fayetteville Formation near center sec. 28, T25N R21E, Craig County (Ketchum 7.5' Quadrangle), Oklahoma, USA; 15.9 km SW of Afton, along Oklahoma Route 82. At stop 2, Norby sampled a 2.1 m exposure of alternating shale and limestone of the upper Fayetteville Formation as samples 5 (upper 1.83 m of limestone) and 6 (0–20 cm of shale near base of exposure) in 1987.

Locality 6 (Oklahoma).—Goddard Formation, Tiff Member, center NW NE NE, sec. 2, T3S R1E, Carter County (Springer 7.5' Quadrangle), Oklahoma, USA (locality data from Lane and Straka, 1974). Locality 65 of Tomlinson (1959, p. 322).

Locality 7 (Illinois).—Ridenhower Formation, partial stratigraphic section sampled midpoint of section line between geographic secs. 3 and 10 (i.e., SW SW SE sec. 3, T2S R9W), St. Clair County (Millstadt 7.5' Quadrangle), Illinois, USA. Outcrop on NE bank of Prairie du Long Creek, just above (N) of old bridge, 1.1 km (0.7 mi) NE of the still-standing (in 1974) old Vogel School. Samples VS-1 (0–0.5 m [0–1.5 ft] above creek level), VS-4 (1.1–1.4 m [3.5–4.5 ft] above creek level), VS-5 (1.4–1.7 m [4.5–5.5 ft]), VS-7 (2.0–2.3 m [6.5–7.5 ft]), and VS-12 (3.5–3.8 m [11.5–12.5 ft]), top of Ridenhower Formation, produced the *Lochriea commutata* elements studied and illustrated in this paper. Vogel School section of Norby (1976) and Norby and Rexroad (1985).

Locality 8 (West Virginia).—Bluestone Formation, Pride Shale Member, Mercer County, West Virginia, USA, at northwest end of Camp Creek Interchange (Exit 20) of the West Virginia Turnpike, 37°29.417'N and 81°06.417'W. Acid residue-derived, fused conodont clusters and discrete conodont elements recovered by Robert Stamm (USGS collection 34004-PC) from a calcareous concretion near the base of the Pride Shale Member. Geographic locality data after Weems and Windolph (1986), who described *Tanypterichthys pridensis*, a paleoniscid fish, from a calcareous concretion from this locality; these authors also provided information regarding the geological setting of the Bluestone and underlying Princeton Sandstone formations.

Locality 9 (Nova Scotia, Canada).—Upper Windsor Group, Herbert River and Kennetcook members, Stewiacke, Colchester County, Nova Scotia, Canada. Samples HerbR-7-7 and Kenk-2-1 are from core from drill hole SB-1 at Stewiacke and processed for conodonts by Weston (1985). Stratigraphic terminology as per Moore (1967), Moore and Ryan (1976),

Geldsetzer et al. (1980), and von Bitter and Moore (1992). Further information regarding drill hole SB-1 may be found in Utting (1980) and von Bitter et al. (2007).

Locality 10 (Schälk, North-Rhine Westphalia, Germany).—Platy limestone (Plattenkalk of Ruprecht, 1937; Horn, 1960; Herdringen Formation of Korn, 2006), previously exposed but now completely covered because of landfill in two abandoned quarries at 51°22.614'N, 7°35.410'E, at Am Schälk, ~1.5 km N of Letmathe, northern margin of the Rhenish Mountains, Germany. Samples Schälk 42 and 50 were collected by Charles Collinson (Illinois State Geological Survey) in June 1964, accompanied by Willi Ziegler and Eva Paproth (Geological Survey of North-Rhine Westphalia at Krefeld). Sample Schälk 42 was collected from a 20 cm dark-gray, fine-grained limestone bed in a trenched interval between the northern quarry and southern quarry, ~12 m stratigraphically above the base of the southern quarry. Sample Schälk 50 was collected from a 50 cm thick medium-dark gray, fine-grained limestone bed at or near the base of the northern quarry, that is ~20.5 m stratigraphically above the base of the southern quarry. Viséan-Namurian boundary beds (according to the traditional definition) were present in these quarries, and both samples are apparently of latest Viséan age. Depending on their position in the stratigraphic column and the ammonoids they may have contained, the samples were taken in the *Lyrogoniatites eisenbergensis* Zone or the *Lyrogoniatites*

liethensis Zone of the current ammonoid biozonation (Korn, 1996).

Locality 11 (Hemer, North-Rhine Westphalia, Germany).—The so-called Arnsberger Grauwacke of Serpukhovian age, sampled by Schmidt (1934a, b), was exposed in the now completely landfilled Bröffel brickpit (Ziegeleigrube Bröffel) at 51° 24.066'N, 7°45.114'E, 1 km N of Hemer at the northern margin of the Rhenish Mountains (Schmidt, 1934a; Horn, 1960). According to Schmidt (1934b, p. 77), the best of the conodont bedding-plane assemblages he studied were collected in the '*bisulcatum*-Kieselschiefer' (siliceous shales with *Eumorphoceras bisulcatum* Girty, 1909) that rest on the first prominent graywacke unit. Most or all of his study material was destroyed during World War II, but the 30 cm thick siliceous shale unit was re-collected by Hermann Schmidt and his students in 1956, which formed the basis of a new study by Schmidt and Müller (1964). The Arnsberger Grauwacke of Schmidt (1934a, b) and subsequent authors was like the Plattenkalk of locality 10 (above), a concept used before the introduction of a lithostratigraphic framework based on formations and members, after ca. 1970; thus, Korn (2006) placed the "Arnsberger Schichten," the Arnsberg Layers or Beds, in the Lüssenberg Formation.

Accepted: 11 January 2021