

Reconsideration of the systematics and distribution of the rhynchonellid brachiopod *Atrypa mesacostale* Hall, 1843 from the Late Givetian and Early Frasnian of New York

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ABSTRACT. The internal structures of the rhynchonellid brachiopod *Atrypa mesacostale* Hall, 1843 revealed for the first time, require a complete re-evaluation of its taxonomic status, stratigraphic significance and geographic distribution. Hall's species often mistakenly assigned to the genus *Leiorhynchus* Hall, 1860, is common and stratigraphically restricted to the late Givetian Genesee or Unadilla Formation and the early Frasnian part of the Ithaca Formation (Genesee Group) in central New York. It is designated as the type species of *Katabuporhynchus* n. gen. in the family Platyterorhynchidae Savage, 1996 (revised and elevated to family rank). An earlier rhynchonellid, restricted to the late Givetian Tully Formation in east-central New York, and previously misidentified as *Leiorhynchus mesacostalis*, is described as *E. alaura* n. sp. in the genus *Eumetabolotoechia* Sartenaer, 1975, the type genus of Eumetabolotoechiidae n. fam. Three biostratigraphic zones are proposed: a *Katabuporhynchus mesacostalis* Zone, an *Eumetabolotoechia alaura* Zone, and a late Givetian North American *Eumetabolotoechia* Zone.

KEYWORDS: *Katabuporhynchus* n. gen., Eumetabolotoechiidae n. fam., Givetian, Frasnian, New York State.

RÉSUMÉ. Réévaluation du statut systématique et de la distribution du brachiopode rhynchonellide *Atrypa mesacostale* Hall, 1843 du Givetien supérieur et Frasnien inférieur de l'État du New York. L'étude, pour la première fois, des caractères internes du brachiopode rhynchonellide *Atrypa mesacostale* Hall, 1843 conduit à une entière réévaluation de son statut taxinomique, de sa signification stratigraphique et de sa distribution géographique. L'espèce fondée par Hall, souvent attribuée au genre *Leiorhynchus* Hall, 1860, est commune et restreinte à la Formation Genesee ou Unadilla du Givetien Supérieur et à la partie frasnienne inférieure de la Formation Ithaca (Groupe Genesee) du New York central. Elle est désignée comme espèce-type de *Katabuporhynchus* n. gen. placé dans la famille Platyterorhynchidae, Savage, 1996 (révisée et élevée au rang de famille). Une espèce rhynchonellide plus ancienne, limitée à la Formation Tully du Givetien supérieur du New York est-central et précédemment identifiée erronément sous le nom de *Leiorhynchus mesacostalis*, est décrite comme une espèce nouvelle, *E. alaura*, du genre *Eumetabolotoechia* Sartenaer, 1975, désigné comme genre-type de la nouvelle famille Eumetabolotoechiidae. Trois zones biostratigraphiques sont proposées: une Zone à *Katabuporhynchus mesacostalis*, une Zone à *Eumetabolotoechia alaura* et une Zone à *Eumetabolotoechia* du Givetien supérieur d'Amérique du Nord.

MOTS-CLÉS: *Katabuporhynchus* n. gen., Eumetabolotoechiidae n. fam., Givetien, Frasnien, État de New York.

1. Introduction

As emphasised by Sartenaer (1980, pp. 17-18), *mesacostalis*, despite its general assignment to the genus *Leiorhynchus*, is a species that contains all five characteristics of a badly defined rhynchonellid species: these are outdated founding, scanty original description, super-abundant mention in subsequent literature, long stratigraphic range – allegedly Eifelian? to Upper Mississippian – and record from several States of the United States of America (Arkansas, Kentucky, Maryland, Nevada, New Mexico, Ohio, Oklahoma, Pennsylvania, West Virginia) as well as various regions of the world [Canada, western Europe, Russia (Arctic region, Timan, Urals, Kuznetsk Basin), N and C Africa].

Following his 1961 revision of the genus *Leiorhynchus* Hall, 1860, Sartenaer proposed many new Devonian genera with type species previously assigned to it (Sartenaer, 1996 gave a list of 23 of them, and mentioned 24 species, including *mesacostalis* still erroneously assigned to *Leiorhynchus*), and progressively restricted its systematic status, its stratigraphic range, and its geographic distribution.

It became evident that the following expressions, often used in the world literature dealing with the Devonian and Lower Carboniferous, were devoid of any sense: *Leiorhynchus* zone, fauna, subfauna, community, assemblage, phase, horizon, bio-facies, bed(s), bearing beds (shales, strata), layers, Schichten, dominated fauna.

When Hall (1867, pp. 353-356) commented on the species assigned to the genus *Leiorhynchus* in south-western New York, species he had already described in 1860 (pp. 75, 85-86), he wrote: "These shells are at present known only in the Hamilton and Chemung groups; beginning their existence in the Marcellus shale, being quite abundant in some dark shaly beds in the middle of the group and in the Genesee slate, and occurring generally in the more shaly portions of the Chemung group".

Williams (1884, pp. 14-16) went a step further in suggesting that "a comparative study of the specimens from various stages in

the Devonian has led me to regard all the species of *Leiorhynchus*, in the New York Devonian at least, as varieties of a common form, whose plasticity has not permanently ceased at any of the horizons in which it occurs", and in being led to believe that "the representatives of the genus *Leiorhynchus*, found in the Devonian of New York at least, offer no better claim to specific distinction than do the various forms of *Atrypa reticularis*, although the variations of form and the relative prevalence of certain variations are valuable and, we believe, sensitive indicators of changed conditions of the environment."

After such statements the door was wide open for the recognition of various Upper Devonian rhynchonellid zones in south-western New York based on the genus *Leiorhynchus* or to species assigned to it, such as *L. globuliformis* (Vanuxem, 1842), *L. laura* (Billings, 1860), *L. mesacostalis* (Hall, 1843), *L. multicostatus* Hall, 1860, *L. quadracostatus* (Vanuxem, 1842), and *L. sinuatus* Hall, 1867.

Sartenaer indicated in various publications that the assignment of Frasnian species to the genus *Leiorhynchus* was incorrect (1968b, p. 6; 1996, pp. 246-247). Following the latest international decision on the Givetian/Frasnian boundary, the Frasnian record of the genus had to be abandoned (Sartenaer, 1983, p. 43; 1984, p. 6; 1985, p. 314; 1987b, pp. 125, 128, 132; 1995, p. 119; 1996, p. 247), because the only New York representative of the genus was its type species, the uppermost Givetian *L. quadracostatus*. He also proposed the establishment of a late Givetian North American *Leiorhynchus* Zone (1996, pp. 245, 247).

In consequence, *Leiorhynchus* has to be replaced by an appropriate genus in the following expressions: *L. globuliformis* (zone, stage), *L. laura* (zone, assemblage, community), *L. limitaris* (zone, community, assemblage, facies), *L. mesacostalis* (zone, fauna, group, beds), *L. multicostatus* (zone, community, assemblage, fauna, group). This substitution already took place for *globuliformis* that is assigned to the genus *Caryorhynchus* Crickmay, 1952 in recent literature, and for *laura* and *limitaris* that

have been revised and designated the type species of the genera *0Eumetabolotoechia* Sartenaer, 1975 and *Cherryvalleyrostrum* Sartenaer, 2004, respectively.

In the present paper *Atrypa mesacostale* Hall, 1843 is assigned to *Katabuporhynchus* n. gen. The range of the species in New York is restricted to the late Givetian Genesee or Unadilla Formation and to the early Frasnian part of the Ithaca Formation (Genesee Group). The earlier form restricted to the late Givetian lower Tully Formation and misidentified in the literature as *mesacostalis*, is assigned to *Eumetabolotoechia alaura* n. sp.

2. Systematic paleontology

All specimens were whitened with ammonium chloride prior to photography and are deposited, with the exception of specimens already figured in the literature, in the Operational Directorate Earth and History of Life (including ex Department of Paleontology) of the Royal Belgian Institute of Natural Sciences, Brussels, abbreviated IRScNBa.

2.1. Family *Platyterorhynchidae* Savage, 1996 (ex *Platyterorhynchinae* Savage, 1996, p. 254)

Composition of the family: *Platyterorhynchus* Sartenaer, 1970; *Hadrotatorhynchus* Sartenaer, 1968a; *Katabuporhynchus* n. gen.

Type genus: *Platyterorhynchus* Sartenaer, 1970

Diagnosis. Shell medium to large size, slightly globulose. Inequivalve with transversely oval to elliptical, sometimes subcircular, outline. Hinge line short. Sulcus and fold well marked, starting at variable distances from the beaks. Sulcus shallow to moderately shallow, moderately wide at front. Tongue and fold moderately high. Maximum thickness located at front margin (crest of tongue) or posterior to it. Moderate number of low, rounded (or angular with rounded top) to flat-rounded costae, starting at variable distances from the beaks. Divisions and intercalations present in median costae. Parietal costae only exceptionally present. Lateral costae, when present, simple, very weak, evanescent posteriorly. Wide apical angle. Shell thick posteriorly. Dental plates well marked (type genus) or inconspicuous or vestigial. Teeth short and stout. Septum long, lamellar. Hinge plate undivided with a small or insignificant crural trough. Dental sockets small (short and narrow). Crura raduliform, rounded to suboval in proximal section.

Discussion. The subfamily *Platyterorhynchinae* Savage, 1996 of the family *Leiorhynchidae* Stainbrook, 1945 is here elevated to family rank and thus removed from the *Leiorhynchidae*. Of the three genera assigned to the subfamily by Savage (1996, table 8, p. 259; 2002, pp. 1154, 1156), only the early Frasnian-late Givetian type genus *Platyterorhynchus* belongs in the family *Platyterorhynchidae*; early Famennian genera *Stenaulacorhynchus* Sartenaer, 1968a and *Insignitisinurostrum* Sartenaer, 1987 are here excluded. However, the late Givetian genus *Hadrotatorhynchus* Sartenaer, 1986, assigned by Savage (1996, table 8, p. 259; 2002, p. 1136) to the subfamily *Leiorhynchinae* Stainbrook, 1945, and the late Givetian-early Frasnian genus *Katabuporhynchus* n. gen are included in the family *Platyterorhynchidae*.

The external and internal characters of the genera *Stenaulacorhynchus* and *Insignitisinurostrum*, which are very different from each other, preclude their inclusion in the family *Platyterorhynchidae*. Both genera have low valves completely covered with costae, starting at the beaks (the costation pattern is not the same in both genera), well marked lateral costae, when present, sometimes absent in *Stenaulacorhynchus*; and a thick septum. *Stenaulacorhynchus* has simple median costae, well developed dental plates, and a covered septalium. *Insignitisinurostrum* lacks dental plates, shows divisions in the lateral costae, and has a very shallow and wide median depression in the hinge plate that is partly covered by projections starting from its edges; this is shown in Cooper & Dutro (1982, in section 24 of plate 40) and in a transverse serial section made from one specimen (not published) by the author.

Also neither genus shows the strongly biconvex profile advocated by Savage (1996, p. 254; 2002, p. 1133) for the

family *Leiorhynchidae*, nor do they have the diagnostic uneven costae and the dental plates almost meeting ventrally of the subfamily *Platyterorhynchinae* Savage, 1996. Membership in the family *Leiorhynchidae* should be restricted to genera with globular shapes, subrounded outlines, thin shells, slender internal structures, wide umbonal cavities, etc. as defined by the type genus *Leiorhynchus*.

Katabuporhynchus n. gen.

Harrington (1966a, 1966b, 1967) questioned Hall's (1860 etc.) assignment of *Atrypa mesacostale* Hall, 1843 to the genus *Leiorhynchus* and assigned the species to the genus *Camarotoechia* Hall & Clarke, 1893, and later, in the final presentation of his PhD at Cornell University, Ithaca (1968), designated it as the type species of *Anodontoplax* n. gen. Subsequently Harrington (1970, 1972) and Harrington & Heaslip (1978) returned the species to the genus *Leiorhynchus*.

Derivatio nominis. *Καταβουπος*, *ου* (*ό*) (Greek = cascade). The name draws attention to the cascades in Fall Creek and Cascadilla Creek, and adjacent gorges in Ithaca that constitute the type area of the Ithaca Formation.

Type species: *Atrypa mesacostalis* Hall, 1843.

Species assigned to the genus. Besides the type species, early Frasnian specimens from British Columbia, Canada, that were informally called *Platyterorhynchus palustris* by Sartenaer (1983, p. 46; 1985, p. 315) are assigned to the genus (see details below).

Diagnostic features. Shell medium to large size, moderately gibbous. Outline transversely oval to elliptical. Hinge line and ventral interarea short. Shell thickest at front margin or posterior to front margin. Sulcus, fold, and median costae starting at or very close to the beaks. Apical angle very wide. Costae in moderate number; median costae commonly divided or intercalated; parietal costae absent; lateral costae, when present, simple and evanescent posteriorly. Shell thick posteriorly. Delthyrial cavity undulated. Dental plates absent or vestigial. Teeth and dental sockets small. Septum slender. Very shallow median depression in the undivided hinge plate. Crural bases stout. Crura raduliform, closely set. Ventral muscle field slightly impressed.

Description. Shell medium to large size, moderately gibbous. Profile dorsibiconvex (dorsal valve about one and a half to two times the thickness of ventral valve). Flanks of ventral valve sloping gently from the umbonal region to the commissures; flanks of dorsal valve strongly. Outline transversely oval to elliptical. Maximum thickness at front margin or posterior to it. Maximum width around mid-length. Hinge line short. Anterior and lateral commissures sharp; anterior commissure (crest of tongue) slightly serrate; antero-lateral commissures slightly undulated when lateral costae are present; posterior commissure sticking out as a result of the postero-lateral margins of the valves being concave near the commissure. Very wide apical angle. Ventral beak slightly incurved. Ventral interarea very short, low. Sulcus and fold well marked, start very close to the beaks. Sulcus wide, moderately shallow and well delineated; bottom flat to slightly convex, extended dorsally as a moderately high tongue with trapezoidal outline, curving gently and never tending to become vertical in its uppermost part. Top of tongue flat or slightly convex = top of shell or located slightly lower than maximum shell thickness. Costae in moderate number; well-marked median costae [in the type species: 4/3: 8 specimens (18 per cent); 5/4 (= median costae in *fold/sulcus*): 13 specimens (29 per cent); 6/5: 15 specimens (33 per cent); 7/6: 9 specimens (20 per cent)], low, irregular on account of common divisions and intercalations (primary costae wide, divided and intercalated costae narrow), rounded, starting at or very close to the beaks; parietal costae absent; lateral costae in variable number (one to eight in the type species), only present in about one half of the specimens examined, becoming evanescent at various distances from beaks. Shell thick in the cardinal area. Delthyrial cavity undulated. Dental plates absent or vestigial. Teeth short, small,

dorsally directed. Septum slender, lens-shaped in its posterior part. Hinge plate thick, wide, with a shallow median depression corresponding to a crural trough. Dental sockets short and shallow. Crural bases stout. Crura round to suboval in proximal section. Phrygian cap-shaped in distal section, curving ventrally at their distal end, raduliform, closely set. Ventral muscle field narrow, longitudinally elliptical to ovate (width: $\frac{1}{4}$ to $\frac{1}{3}$ shell width; length: slightly more than $\frac{1}{3}$ shell length); very reduced adductor impressions surrounded by large diductor impressions. Dorsal muscle field indistinguishable.

Discussion. The latest Givetian genus *Leiorhynchus* is very different from *Katabuporhynchus* n. gen. The following comparison, in which the genus *Leiorhynchus* is defined by its type species, *L. quadracostatus*, is only made because *mesacostalis* has commonly been included in it.

Katabuporhynchus n. gen. and *Leiorhynchus* have some features in common, e.g. the location of the greatest width of the shell; location of the greatest thickness of the dorsal valve; wide sulcus and fold; the crest of tongue located below the summit of the shell; the anterior commissure slightly serrate, lateral commissures little or not; low, wide, and rounded to flat-rounded costae; small and short teeth; a short "septalium" or "crural trough; and, narrow and elongated dorsal muscle scars.

Leiorhynchus can easily be separated from *Katabuporhynchus* n. gen. by its more inflated aspect; a usually smaller size; an helmet-shaped anterior profile; a rounded to elliptical outline; the length similar to width, and thus, different l/w, t/w, and t/l ratios; sulcus, fold and costae starting at great distances from the beaks; a shallower sulcus; a lower fold; the crest of fold usually slightly convex; a different distribution of the median costae (4/3 in 78 per cent of specimens of *L. quadracostatus*, 18 per cent of specimens of *K. mesacostalis*; 5/4 in 10 per cent of specimens of *L. quadracostatus*, 29 per cent of specimens of *K. mesacostalis*; 6/5 in 5 per cent of specimens of *L. quadracostatus*, 33 per cent of specimens of *K. mesacostalis*); lower median costae; a thinner shell; dental plates separated from the walls of the shell by well developed umbonal cavities; a divided hinge plate; a longer and higher septum; and very different crura (finer, trough-shaped and strongly incurved distally).

Katabuporhynchus n. gen. and the topmost Givetian-lower Frasnian genus *Platyterorhynchus* Sartenaer, 1970 are closely related. They have many characters in common: weakly uniplicate anterior commissure; short hinge line; smoothly rounded lateral margins; shell thickest posterior to front margin; maximum width around mid-length; sharp commissures; anterior commissure (crest of tongue) slightly serrate; antero-lateral commissures slightly undulated by lateral costae, when present; slightly to strongly incurved ventral beak; short ventral interarea bordered by sharp ridges; well marked sulcus and fold; wide, shallow, and well delineated sulcus, extended dorsally as a low to moderately high tongue with trapezoidal outline, curving gently and never tending to become vertical in its uppermost part; bottom of sulcus flat to slightly convex; top of tongue flat or slightly convex, located lower than the maximum shell thickness; a moderate number of low, irregular (common divisions and intercalations), rounded median costae; parietal costae absent; lateral costae, when present, becoming evanescent at various distances from the beaks; short, small and dorsally to dorso-laterally directed teeth; thin septum; thick undivided hinge plate; very shallow and weakly developed septalium; short crural bases; closely-set crura; and, slightly depressed ventral muscular field.

Katabuporhynchus n. gen. differs from *Platyterorhynchus* by its transversely oval to elliptical outline (subrounded in *Platyterorhynchus*), sulcus, fold, and median costae starting at or very close to the beaks, thicker shell; undulated delthyrial cavity; very short, dental plates absent or vestigial, and lens-shaped septum in its posterior part.

Collections from the Canadian Rocky Mountains highlight the similarities and differences between the genera *Platyterorhynchus* and *Katabuporhynchus* n. gen. In Canada *Platyterorhynchus russelli* McLaren, 1962, the type species of the genus, is known to be abundant in four major localities: Gypsum Cliffs on Peace River (type locality) and Birch River in northeast Alberta; Cecilia Lake-Kakwa Lake area in east-central and Nabesche River

area in northeast British Columbia. The following collections of the Geological Survey of Canada examined by the author indicate that most specimens from the Lower Frasnian of British Columbia may reach larger size, have more and slightly more pronounced median costae, and show some of the diagnostic external features (transversely oval to elliptical, seldom subrounded, outline; sulcus, fold and median costae starting at or very close to the beaks) of *Katabuporhynchus* n. gen.:

- GSC loc. 35103. Northeast flank of Wallbridge Mountain near Cecilia Lake, 230 feet above base of Devonian. Collector: D. J. McLaren, 1952. Eighty-three specimens including paratypes G, GSC N°14924 = pl. XVII, fig. 10, H, GSC N°14925 = pl. XVII, figs 3a-c, I, GSC N°14926 = pl. XVII, figs 7a-d in McLaren (1962) as *Leiorhynchus russelli*.

- GSC loc; 35102. Below the saddle at the northeast end of the mountain on the northwest side of Kakwa Lake, from talus collection. "Flume Formation", 186 to 205 feet above base of Devonian section. Collector: D. J. McLaren, 1952. Two specimens. Locality mentioned by McLaren (1962, pp. 100, 120 as *L. russelli*).

- GSC loc. 41321. Near Nabesche River. Argillaceous limestone of "Flume formation equivalent" about 100 feet below shale unit ("Perdrix equivalent"). Collector: A. E. H. Pedder, Triad Oil Company Limited, 1960. Eight specimens. Locality mentioned by McLaren (1962, pp. 100, 122 as *L. russelli*).

- GSC loc. 41320. Nabesche River. Waterways equivalent. Same collector. Eleven specimens.

- GSC loc. C-3144. Section six miles south of the Nabesche River, 441 feet above the base of the "Beaverhill Lake" Formation. Collector: G. C. Taylor, 1968. Identified by A. W. Norris (1972) as *Platyterorhynchus russelli*. One hundred fourteen specimens.

- GSC loc. 57107 Nabesche River, Halfway River map area. Basal Upper Devonian, 1700 feet above base of Middle Devonian carbonate. Collector: E. L. Fitzgerald, Calgary and Edmonton Corporation Limited, 1963. Identified by D. J. McLaren, 1963 as *Leiorhynchus russelli*. Twenty-seven specimens.

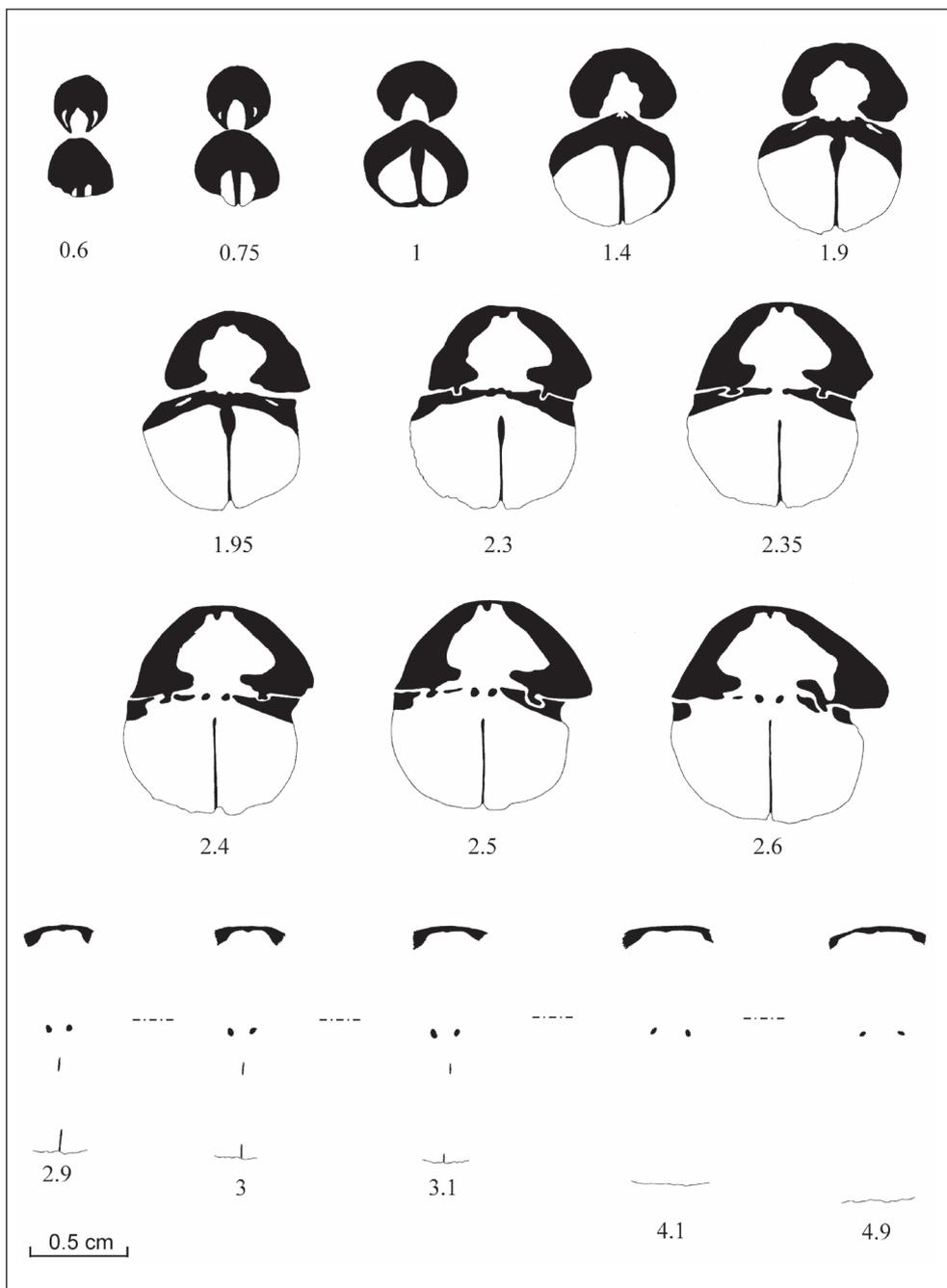
Moreover, serial transverse sections made by McLaren (1962, fig. 28, p. 98) from a specimen from GSC loc. 35103 (= paratype K, GSC N°15206) show some of the diagnostic internal characters (undulated delthyrial cavity; absent or vestigial dental plates; and the lens-shaped posterior part of the septum) of *Katabuporhynchus* n. gen. that stand out in sharp contrast to the sections made by the same author (1962, fig. 28B, p. 78 and fig. 27, p. 97) from a specimen from GSC loc. 29432 (Gypsum Cliffs, north bank of Peace River = paratype J, GSC N°15205). Collector: A. W. Norris, 1956. Locality mentioned by McLaren (1962, pp. 96, 100, 117 as *Leiorhynchus russelli*).

Various authors confirmed the presence of *russelli* in beds of early Frasnian age from British Columbia, e.g. Maurin & Raasch (1972, pl. III between p. 86 and p. 87) in the Kakisa-Cecilia Lake area, Norris (1979, p. A244), and McLean & Klapper (1998, p. 532) at Gas Keg Ridge in the Nabesche River area. The British Columbia representatives of *russelli* were informally called *Platyterorhynchus palustris* by Sartenaer (1983, p. 46; 1985, p. 315); they are preferably called *Katabuporhynchus palustris*.

The close affinity between the genera *Katabuporhynchus* n. gen. and *Platyterorhynchus* explains that one or two external characters of the former may be observed in the latter, e.g. some specimens of *Katabuporhynchus mesacostalis* and *K. palustris* show the characteristic subrounded outline of *Platyterorhynchus russelli*, while some specimens of *P. russelli*, such as paratypes D and F figured by McLaren (1962, pl. XVII, figs 6a-d, 9a-c), show the median costae (slightly more pronounced, and starting nearer to the beaks than in most specimens of the species) of *Katabuporhynchus*.

The late Givetian genera *Hadrotatorhynchus* and *Katabuporhynchus* n. gen. are very similar externally, but very different internally. The genera are similar in the medium to large size, gibbosity of shell; transversely oval to sub-elliptical outline; sharp commissures; slightly serrated anterior commissure; short hinge line; well marked sulcus and fold; moderately shallow sulcus; moderately high fold; moderately high tongue; short ventral interarea; moderate number of costae; and a lamellar septum. *Katabuporhynchus* n. gen. differs from *Hadrotatorhynchus* in its elliptical outline (never subcircular); sulcus and fold starting at or

Figure 1. *Katabuporhynchus mesacostalis* (Hall, 1843). Camera lucida drawings of serial transverse sections; figures are in mm forward of the ventral umbo. IRScNBa12807. Norwich, Genesee or Unadilla Formation, latest Givetian. Width of distorted specimen: 29.9 mm.



very close to the beaks, a narrower sulcus at front, a fold without a slight more or less median depression, and never marked by a sharp increase in height near the front, more pronounced median costae starting at or very close to the beaks, commonly divided or intercalated, less well marked lateral costae, when present, shorter septum, thick undivided hinge plate with a very shallow depression (no actual hinge plate in *Hadrotatorhynchus*, but two depressions separated from a shallow septalium by two marked projections), stout crural bases, and differently shaped crura.

***Katabuporhynchus mesacostalis* (Hall, 1843)**
(Figs 1-2, Pl. 1, Figs A-Bb)

Lectotype selected herein. Hall, 1843, Fig. N°67, 1a (Table of organic remains, p. 60) (AMNH – F130627). It almost certainly came from the Ithaca Formation (Genesee Group) at Ithaca, Tompkins County, N.Y.

Material. About a hundred specimens from the Ithaca Formation in New York: the types figured in various publications by James Hall at the American Museum of Natural History (New York City, N.Y.) and specimens from the National Museum of Natural History (Washington, D.C.), American Museum of Natural

History, Field Museum (Chicago, Ill.), Cornell University (Ithaca, N.Y.), British Museum of Natural History (London, England).

Forty-nine specimens collected by the author in October 1967 under the guidance of John W. Wells: seven from the middle part of the Ithaca Formation from a quarry 0.5 miles south of Asbury, north of Ithaca, N.Y., three specimens from the Triphammer Member of the Ithaca Formation at a roadcut on NY Rte. 13 at the Cortland/ Tompkins County line, four specimens from the lower to middle Ithaca Formation at Cascadilla Creek, Ithaca, N.Y., and thirty-five specimens from a fossiliferous sandstone, probably Sherburne equivalent, Givetian, at Fall Creek, 3 miles west of Cortland, N.Y.

One hundred and three specimens from Norwich, Genesee or Unadilla Formation, latest Givetian, collected by the author in May 1959 under the guidance of G. Arthur Cooper.

Fifty-six per cent of specimens are isolated ventral or dorsal valves, 44 per cent are articulated but most are crushed and distorted. Most of the specimens are internal moulds. The shell around the umbonal region is preserved in exceptional cases.

Diagnosis. Hall’s brief explanation of figure N°67 (p. 60 in Tables of organic remains) draws attention to the major external feature of his species *mesacostalis*: “four to six strong ribs along

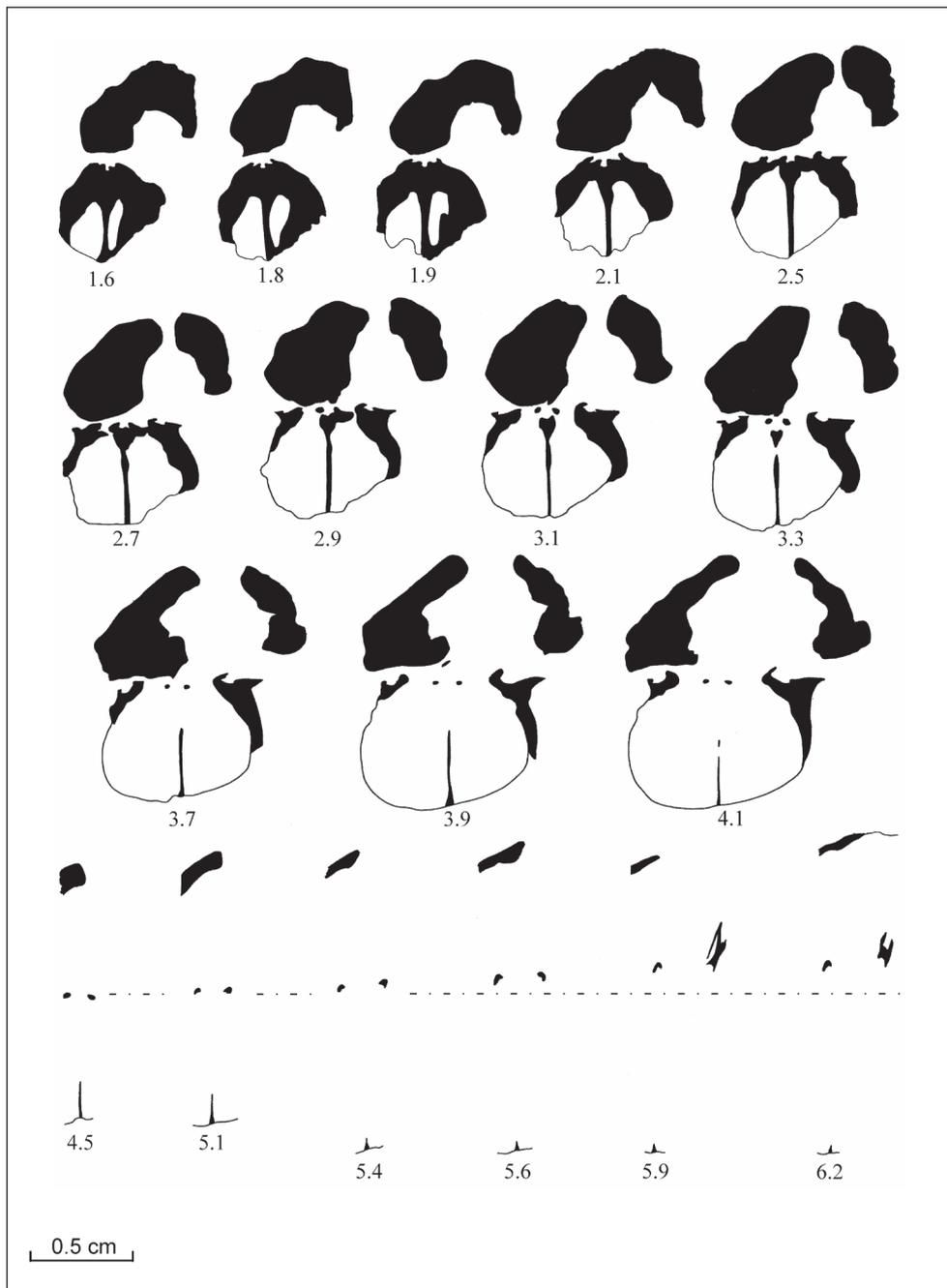


Figure 2. *Katabuporhynchus mesacostalis* (Hall, 1843). Camera lucida drawings of serial transverse sections; figures are in mm forward of the ventral umbo. IRScNBa12832. Quarry 0.5 miles south of Asbury, north of Ithaca, middle part of Ithaca Formation. Measurements: length: (26.3 mm); width: 34.6 mm; thickness: (21.7 mm).

the mesial elevation and depression of either valve, while they become obsolete towards the margins”.

Description. The three specimens of the type series come from the Chemung Group and belong to three different genera (*Remark:* Chemung is no longer a valid stratigraphic name, just a facies name. When Hall says Chemung at Ithaca, where the lectotype comes from, he means the Ithaca Formation).

The specimen of figure N°67, 1a (posterior view, p. 60 in Tables of organic remains) of 1843 (= fig. 1a, p. 86 of 1860 = pl. LVII, fig. 20 of 1867 = pl. 83, fig. 12, p. 188 in Linsley, 1994) [AMNH (American Museum of Natural History, New York) – FI30627] is the only one coming from the locality Ithaca mentioned by Hall (1843, p. 60). It is also the only one corresponding to the original definition of the species, which is further illustrated by figures 21 to 25 of plate LVII of 1867 (= pl. 83, figs 6-9, 13 in Linsley, 1994). It is the only bivalved specimen ever figured by Hall (1843; 1860; 1867), although entire casts are common, as observed by Hall himself (1867, p.363); a lateral view would have allowed to see the characteristic profile of the species, which can only be suspected in the posterior view offered. This specimen is here formally designated the lectotype of the species.

The specimen of figure N°67, 1 (ventral view, p. 60 in Tables of organic remains) of 1843 (= fig. 1, p. 86 of 1860) (AMNH – FI30627) is a large specimen, larger than any specimen of *mesacostalis*, with flanks completely covered with costae, contrary to the “plain or obscurely marked lateral costae” advocated by Hall (1860, p. 86) and the “lateral portions of the fossil...essentially free from plications, but...sometimes visible” mentioned by Hall (1867, p. 363). The “elongate” outline of this specimen, indicated by Hall (1860, p. 86) is never observable in specimens of *mesacostalis*; Hall (1867, p.363) indirectly admitted this mistake in correctly describing the outline of *mesacostalis* as “oval or ovate”. This paralectotype (A) shows some analogy to large specimens assigned in the literature to *Leiorhynchus multicostus*, a species also in need of a full revision.

The specimen of figure N°67, 1b (ventral view, p. 60 in Tables of organic remains) of 1843 (= fig. 1b, p. 86 of 1860 = probably pl. LVII, fig. 19 of 1867 = pl. LIX, fig. 11 in Hall & Clarke, 1893 = pl. 83, fig. 11, p. 188 in Linsley, 1994) (AMNH – FI37639), considered as a “young individual” by Hall (1860, p. 86) or “small individual” by Hall (1867, explanation of figure), with flanks also completely covered with costae, has an outline never observed in juvenile specimens of *mesacostalis* that have the same outline as adult specimens of the species. This paralectotype (B) that

differs from the lectotype by a smaller size, a lesser thickness, a subpentagonal outline, and numerous costae covering the whole shell, is the one that must have influenced Cooper (1933), when he recognized for the first time the presence of *mesacostalis* in the Tully Formation. Still, it cannot be a representative of the new genus and new species from the Lower Tully Formation described in the present paper, because all localities mentioned by Hall in 1860 (Steuben county, and other parts of Western New York) and 1867 (near Ithaca; at Chemung and Chemung narrows; near Elmira; and Bath, all localities considered to be in the central part of the State) are located in southwestern New York, where the Tully Formation is absent, with the exception of Trumansburg. It is also unlikely that it could come from a locality included in the “&c” mentioned in 1843, and in the “numerous localities in the central part of the State” and “etc” mentioned in 1867, because these localities are also in the Chemung Group at or west of Ithaca in central New York as this part of the State is named by Hall. Paralectotype B is a juvenile specimen or a full size representative of one of the species of the Chemung Group as understood by Hall in the middle of the nineteenth century. Specimen of plate LVII, fig. 18 of 1867 (= pl. 83, fig. 10, p. 188 in Linsley, 1994) also belongs to such a species. On the whole it is surprising that Hall established the species on such poor grounds when it is obvious that abundant specimens of the species, based on its lectotype, were present, many of them complete, although crushed, in many outcrops available and untouched at that time. Such specimens were collected in abundance by Kindle (1896), who studied ten “Ithaca sections” in the “numerous deep gorges of the streams entering the Cayuga valley” that “afford excellent exposures of the rocks about Ithaca, “from the base of the Portage to the top of the Ithaca group” (p.16).

Specimens figured by Hall (1867), other than those of the type series. See Pl. 1, Figs B-F, Pl. 2, Fig. Ll.

Generic characters in need of further detail. Width of sulcus at front between 44 and 75 per cent (mostly between 56 and 65 per cent) of shell width. The number and distribution of median costae, and the number of lateral costae have been mentioned above. Average width of 17 large specimens (29.1 mm) (Lectotype: 31.8 mm); average length measured of nine large specimens (24.2 mm); average (approximate) thickness of five large specimens (15.2 mm). Width and thickness of middle-sized specimens between 24.5 to 27 mm, and between 16.6 and 18.1 mm, respectively. l/w ratios in large specimens: 0.75 to 0.94 (most 0.81 to 0.91); t/w ratios in large specimens: 0.40 to 0.53 (most 0.44 to 0.53); t/l ratios: 0.44 to 0.78 (most 0.49 to 0.78). Apical angle between 123° and 130°. Transverse serial sections from two specimens are shown in Figs 1, 2.

Discussion. Although extremely brief, Hall’s (1843, Tables of organic remains, p.60, N°67, 1, 1a,b), the definition of the abundant New York species, *Atrypa mesacostalis* Hall, 1843, refers to the locality (Ithaca), the stratigraphic position (Chemung), and some major external features of the species: “four to six strong ribs along the mesial elevation and depression of either valve”. The name of the species draws attention on the character and number of median costae. With its four to six median costae and weak lateral costae described by Hall (1860; 1867; see above). *Katabuporhynchus mesacostalis* is easily distinguished from the Givetian [Four ribbed orthis (*O. quadricostata*) Vanuxem, 1842 (later *Leiorhynchus quadracostatus*), *L. multicostus*, *Rhynchonella* (?) *Laura* (now *Eumetabolotoechia laura*), *L. dubius* Hall, 1867, *L. Huronensis* Nicholson, 1874 (now *Eumetabolotoechia huronensis*) and Frasnian (*L. sinuatus*) species introduced around the middle of the 19th century.

Why then has the species commonly been mistaken for one or another of the species just mentioned, and given a considerable stratigraphic range and geographic distribution?

The responsibility lies partly with Hall himself, who reduced to a minimum the original description and illustrated it by poor lithographs. A slightly longer description, with the same lithographs, was proposed by Hall (1860, p.86, figs 1, 1a,b), but it is only seven years later than Hall (1867, pp.362-363, pl. LVII, figs 18-25; fig. 23 = fig. 12 in Hall & Clarke, 1893) gave an extended description of the species and figured eight specimens. Most of

these figures indicate that better specimens than those figured by Hall (1843, table of organic remains, figs N°67, 1, 1a,b) were present in the almost untouched and numerous outcrops available in the middle of the 19th century.

The short original description of *mesacostalis*, combined with poor illustration, opened the door to comparisons with many species; most of them assigned today to genera other than *Leiorhynchus*. Suffice it to give some examples of the misconception of the species in the New York State literature, starting with its founder (Hall, 1867, pp. 359-360, 363, 370), who did not consider it himself as clear-cut. This is also true for *multicosta* and *globuliforme*: “*L. multicosta* in the Hamilton shales and *Rhynchonella? Laura* from Bosanquet and Widder in Canada West present considerable variety in their surface characters”, “were they [specimens from Widder] imbedded in an argillaceous shale instead of a calcareous one, they would not be different in appearance from *L. quadricostata*”, and “Altogether accepting for the present the distinction between these forms, I believe they will prove identical; and I am not indisposed to unite with these *L. mesacostalis* of the Chemung group” (pp.359-360); “I am quite prepared to see the propriety of uniting it [*L. mesacostalis*] with the species just named [*L. quadricostata*], and perhaps even with *L. multicosta* of the Hamilton group” (p.363); It is possible that larger collections may show the propriety of uniting these [a few individuals of *L. globuliformis*] with *L. mesacostale*” (p. 364).

Other examples are to be found in Girty, and Williams: Girty (1909, p. 27), describing *Leiorhynchus* aff. *mesicostale* (converted by him, in 1911, in *L. carboniferum* Girty, 1911) from the Caney shale (Lower Mississippian), adopted Hall’s views on plication: “in both *L. laura* and *L. quadricostatum* a strong tendency is manifested for the lateral plications to die out partially or entirely, thus grading into *L. mesicostale*”; Williams (1884, p.14; 1887, pp.61, 80), referring to specimens of “*Leiorhynchus mesocostalis* and varieties” in the Portage fauna on “opposite sides of the valley in which Ithaca is situated”: he mentions the occurrence of specimens “which present more or less fully the distinctive characters of *L. limitaris*, of *L. quadricostata*, or of *L. mesocostalis*” (p. 14); “*Leiorhynchus* varying ...from *L. multicosta* to *L. mesocostalis*, was seen” in “more shaly strata” of the Chemung in the Genesee Section at Caneada Creek, below East Rushford (p.61); “*L. multicosta*, running into the form of *L. mesocostalis*” at Hornellsville, Steuben County, in a “like a forerunner of the Chemung fauna” (p.80).

As for the species described as *Eumetabolotoechia alaura* n. sp. in the present paper, Cooper & Williams (1935, p. 822) wrote that *Leiorhynchus mesacostalis* of the Tully fauna “is sometimes indistinguishable from *L. multicosta* of the Hamilton region”.

Aside from the three completely different specimens supposed to illustrate the species, the original description of *mesacostalis*, although too short, is very explicit. It is restricted to the costation of the shell that is, therefore, the only characteristic feature of the species brought forward: “Shell with from four to six strong ribs along the mesial elevation and depression of either valve, while they become obsolete toward the margins”.

The lectotype is the only specimen of the type series that is in accordance with this description. Its designation in the present paper should allow identifying the species without any difficulty in the future.

Leiorhynchus quadracostatus (Vanuxem, 1842) from the top of the Genesee Shale at the base of the Genesee Group and the base of the Sherburne Flagstone with its consistent four median costae from which it gets its name, differs also in its greater gibbosity and subcircular outline (oval to elliptical in *K. mesacostalis*) Also internally *L. quadracostatus* has a thinner shell; dental plates separated from the walls of the shell by well developed umbonal cavities (vestigial in *K. mesacostalis*); straight or slightly convex dental plates (undulated in *K. mesacostalis*); a “crural trough” that is clearly marked; and trough-shaped crura distally (simple, rod-like, and round to suboval in section in *K. mesacostalis*).

Range and distribution. *Katabuporhynchus mesacostalis* is an abundant New York species qualified for a long time as “characteristic of the Chemung” (Newberry, 1873, p. 164); “part of the Ithaca fauna proper around Ithaca” (Williams, 1884, p. 19); “one of the species typical of the Ithaca shale” (Kindle, 1896, p.

20), “authentic [specimens] from the Ithaca formation at Ithaca” (Prosser, C.S., 1912, p. 285); “guide fossil”, “index form”, “typically Ithaca” (Chadwick, 1934, p. 351); “Ithaca fossil” or “Ithaca type” (Cooper & Williams, 1935, pp. 804, 805). Cooper & Williams (1935, p. 822) even considered the species as an “Ithaca element” of the Tully fauna following their acceptance of the presence of *mesacostalis* (the Tully “*mesacostalis*”) in the Tully Formation.

K. mesacostalis has a short range in a restricted area of central New York. The range of the species is from the upper Givetian Genesee or Unadilla Formation to the top of the Triphammer Member of the lower Frasnian Ithaca Formation that is subdivided into three members: from base to top, Cascadilla, Treman, and Triphammer members. The species is particularly abundant in the lower Cascadilla Member, and in the transition beds between the Treman and Triphammer members. The Triphammer Member, as here understood, has recently been subdivided by Zambito et al. (2009) into a lower Triphammer Member and an upper Cayuga Heights Member.

K. mesacostalis is known from collections and literature reports at many localities in and around Ithaca in Tompkins County, including Fall Creek, Cascadilla Creek, Buttermilk Creek, on Rte. 34A, just south of West Clinton Street, Glenwood Creek, Newfield Creek, Renwick Brook, Williams Creek, and various quarries (all long abandoned) including Hazen Street, 0.5 mi south of Asbury, McGraw-Fiske, University, and Cornell. In the southern part of Cayuga County it occurs at Long Hill Road, 1¼ mi and 2 mi northwest of Moravia, Gate Road, 2 mi southeast of Moravia, Iowa Road and Scott Gulf, 2 mi east of Sempronius, and 1½ mi northeast of Wilson Corner. It occurs also at the Tompkins/Cortland County line (on Rte. 13, 1½ mi east of Dryden, in Cortland County (near Blodgett Mills; quarry on Rte. 90, 1 mi south of Cortland; outcrop on Rte 81, 4 mi south of Cortland; Homer Gulf, 1 mi and 1½ west of Rte 41; Cincinnatus) and in the western part of Chenango County (Norwich Pitcher).

A *Katabuporhynchus mesacostalis* Zone is proposed. The presence of the species at various stratigraphic levels, different from the one here indicated, is discussed below.

The *Caryorhynchus globuliforme* and *Leiorhynchus* (?) *mesacostale* Zone is one of the five (“at least”) “well-defined rhynchonellid zones” distinguished in the New York Senecan by Harrington (1972, p. 278, fig. 1, p. 279, p. 281). It falls “within” the *Manticoceras simulator* and *Probeloceras lutheri* goniatite zones (I(β)γ), and the species characterizing the zone are “commonly associated” with *Hadorrhynchia* (?) sp. cf. *H. solon* (Thomas & Stainbrook, 1924) (*Remark: globuliforme sensu* Harrington does not correspond to *globuliforme* defined by Vanuxem). Rickard (1975, pl. 3) adopted the zone, and Norris (1979, fig. 7, p. A241) referred to it. Rickard in Kirchgasser et al. (1985, table 7, p. 248) split the zone into three zones: a lower *Leiorhynchus?* *mesacostale* brachiopod zone developed in the Lower *Polygnathus asymmetricus* Zone, and an upper *Caryorhynchus globuliforme* Zone developed in the Middle *Polygnathus asymmetricus* Zone, separated by an *Hadorrhynchia?* sp. cf. *solon* (“*Rhync. pugnus*”) Zone developed in the middle and upper Lower *Polygnathus asymmetricus* Zone. Rickard indicated on the same table the presence of *Leiorhynchus?* *mesacostale* in the uppermost part of the Hamilton Group and in the Tinker Falls, New Lisbon, Apulia, and Laurens members of the Tully Formation. These four members contain the Tully “*mesacostalis*” described as *Eumetabolotoechia alaura* n. sp. in the present paper.

Varieties have been sometimes mentioned in the literature without further precision, e. g. by Williams (1884, p. 14 as varieties) in a Portage fauna on “opposite sides of the valley in which Ithaca is situated”, and by Kindle (1896, p. 20 as a small variety) in the Ithaca shale of the Cascadilla Creek, Ithaca.

As a result of the poor original definition of the species, its “migration” from central New York to other regions (other States of the United States of America, Provinces of Canada, and various other countries in the world) has been favoured (see Appendix).

The presence of *mesacostalis* in the Tully Formation (at the base of the Upper Devonian Portage Group) is discussed below.

The presence of *mesacostalis* in Pennsylvania will have to remain an open question. The species has often been reported in the literature from the Hamilton, Sherburne, Portage, and

Chemung, e.g. Lesley (1889-1890, pp. 306-307 as *Leiorhynchus mesacostale*), Chemung beds, Center, Columbia, Crawford, Erie, and Perry counties; Kindle in Williams & Kindle (1905, pp. 69, 71, 72, 73, 76, 77, table between p. 78 and p. 79, pp. 89, 114, chart, p. 116 as *L. mesicostale*), Hamilton and Sherburne, Columbia County (Catawissa, East Bloomsburg), and Chemung, Tioga County (Tioga); Williams in Williams & Kindle (1905, pp. 84-85 as *L. mesicostale*), fauna typical of the Ithaca Member, Catawissa; and Willard [1939 as *Liorhynchus mesacostale* and *L. cf. mesacostale*, p. 186 (Ludlowville faunal element of the Mahantango Formation at the top of the Hamilton Group), p. 213 (Trimmers Rock fauna of the Fort Littleton Formation at the top of the Portage Group), p. 214 (a fauna in Pine County with “pronounced Ithaca affinities”), p. 249 (Wellersburg Formation at the top of the Chemung Group). Three specimens were figured by Willard (1939, pl. 19, figs 29-31): the ventral and the dorsal view (figs 29, 30) of two specimens from the Chemung Group at Manns Choice, Bedford County, SW Pennsylvania, and the ventral view (fig. 31) of a specimen from the Losh Run shale? (member of the Fort Littleton Formation at the top of the Portage Group; probably Sherburne) at 6.1 mi east of Northumberland, Northumberland County, EC Pennsylvania. Costation alone allows stating that the specimens from the Chemung Group do not belong to *mesacostalis*, but the specimen from the Portage Group shows the common costation of specimens of the species. Therefore the presence of *mesacostalis* in Pennsylvania cannot be disregarded; the destruction by fire of the collections of the Pennsylvania Geological Survey precludes any further observation.

Observations made by the author on collections he had the opportunity to examine in various museums, universities, and scientific institutions (see above) and on his own material indicate that specimens of *mesacostalis* are large in the upper part (lower Triphammer Member), and of medium size (Pl. 1, Figs S-Bb) in the lower part (lower Cascadilla Member) of the stratigraphic range of the species. Medium-sized specimens have less median costae and divisions; they probably correspond to the small variety mentioned by Kindle (1896, p. 20) in the Ithaca shale of Cascadilla Creek, Ithaca. The restricted field experience of the author in southwestern New York makes the proposal of a subspecies or a new species taxonomically and stratigraphically inappropriate. Only careful collecting with this problem in mind could give some credit or invalidate such an opinion. The existence of ecological variants cannot be disregarded.

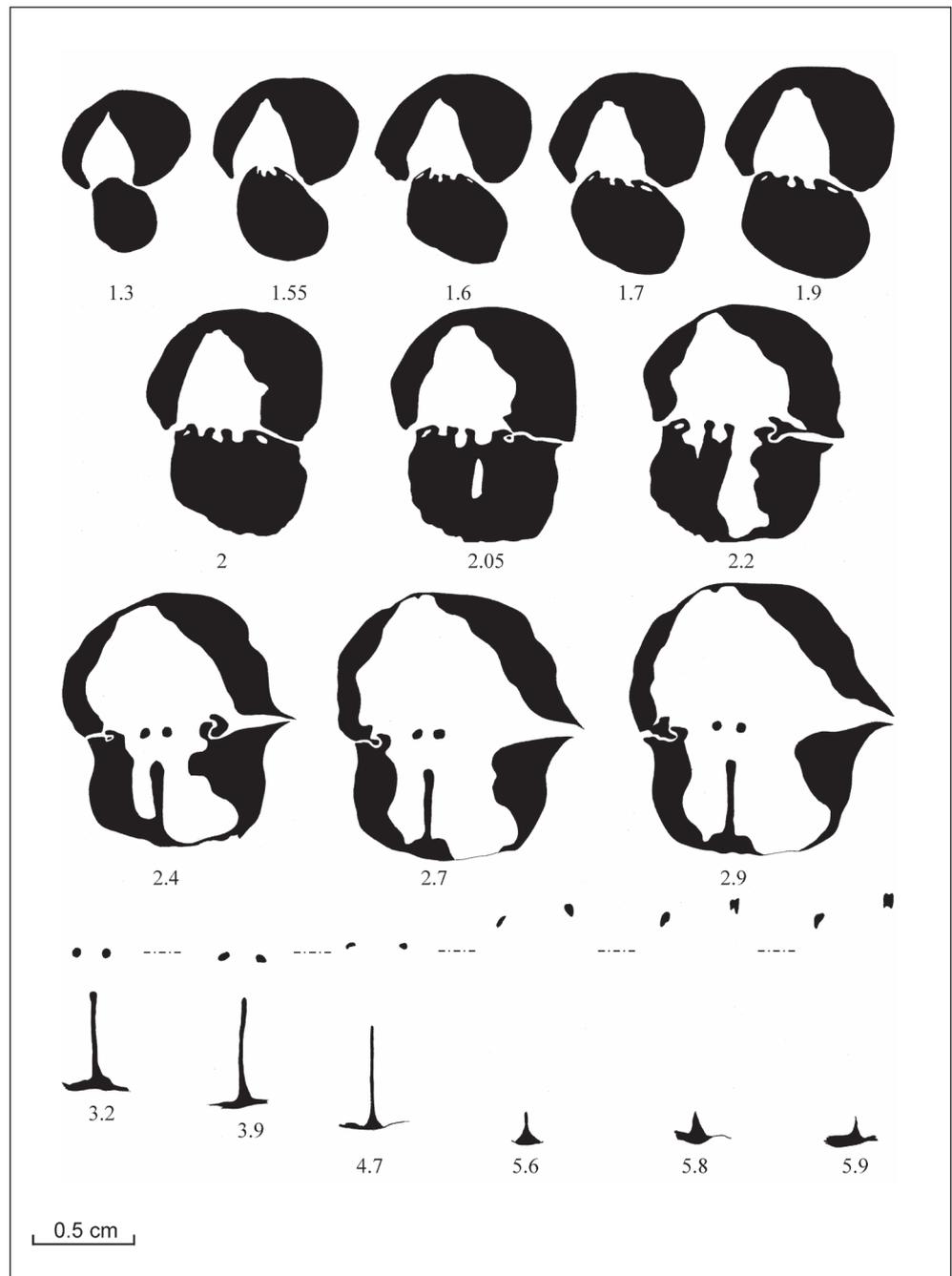
2.2. Family *Eumetabolotoechiidae* n. fam.

Type genus: Eumetabolotoechia Sartenaer, 1975

Diagnosis. Size medium (generally) to large. Profile lens-shaped. Outline longitudinally subovate. Hinge line and ventral interarea short. Commissures sharp, slightly to very slightly undulated by the costae. Sulcus and fold well marked, starting near to the beaks. Sulcus shallow with variable width at front. Fold low. Tongue low to moderately high, trapezoidal, stretched anteriorly. Maximum width generally located around the anterior third of length, sometimes around mid-length. Maximum thickness located generally slightly posterior to the front margin, sometimes at front margin. Apical angle moderately wide. Costae in moderate number, low rounded (or angular with rounded top) to flat-rounded, of variable width. Median costae starting at or very near to the beaks, irregular on account of common divisions and intercalations. Lateral costae simple, exceptionally divided, starting in the umbonal regions. Parietal costae rare. Shell thick posteriorly. Dental plates residual or absent. Teeth small, simple, stout. Dental sockets narrow. Septum long, strong posteriorly, growing thinner anteriorly. Hinge plate thick with a median crural trough. Crural bases robust. Crura long, raduliform, crescent-shaped to Phrygian cap-shaped in section, recurved at their distal end.

Discussion. The new family differs from the family Platyerorhynchidae by a generally medium size; a lens-shaped profile; a longitudinally subovate outline; sulcus and fold always starting at or very near to the beaks; a moderately wide apical

Figure 3. *Eumetabolotoechia alaura* n. sp. Camera lucida drawings of transverse serial sections; figures are in mm forward of the ventral umbo. Paratype J, IRScNBa12816. Houghtaling's Glen, 1½ mi NE of Laurens, Otsego County, Laurens Member of the Tully Formation. Measurements = length: 22.5 mm; width = 20.4 mm; thickness = 14.4 mm.



angle; the maximum width generally located around the anterior third of length; and, lateral costae always present, starting in the umbonal regions. Internal differences are less numerous. In the family Eumetabolotoechiidae, the hinge plate is divided (*Remark: Eumetabolotoechia laura* and *E. alaura* n. sp. show some differences, e.g. there is no actual hinge plate in *E. alaura* n. sp.), a septalium is present, crura are crescent-shaped to Phrygian cap-shaped in section, and, although the septum is long with a lamellar border in both families, it is thick and lens-shaped at its base in the family Eumetabolotoechiidae.

Genus *Eumetabolotoechia* Sartenaer, 1975

Type species: Rhynchonella (?) Laura Billings, 1860

***Eumetabolotoechia alaura* n. sp.**
(Fig. 3, Pl. 2, Figs A-I)

Remark. Johnson (1970, pp. 2100, 2102) stated that he “followed Cooper and Williams (1935) in applying the name [*mesacostale*] to a Tully fossil. Eventually this species must be restudied and assigned to another genus, possibly *Caryorhynchus*, or to a new genus”.

Derivatio nominis. A = privative prefix followed by *laura* to differentiate the new species from *E. laura* (Billings, 1860) from the Upper Givetian of southwestern Ontario, Canada and often incorrectly mentioned in the literature as present in New York.

Material. One hundred and ninety-seven specimens: 87 specimens from the Otego Valley (Houghtaling's Glen, 1½ mi north-east of Laurens; Laurens Member of the Tully Formation); 110 specimens from the Butternut Valley [75 specimens from the first south tributary to Stony Creek (upper part of New Lisbon Member, *sensu* Cooper & Williams, of the same formation); 25 specimens from an outcrop one mi east of Portlandville (Laurens Member of the same formation); and 10 specimens from a quarry, 1½ mi east of New Lisbon (base of Laurens Member of the same formation)].

With the exception of two specimens, one from Houghtaling's Glen, the other from a quarry 1½ mi east of New Lisbon figured by Cooper & Williams (1935, pl. 57, fig. 16 = dorsal view, designated in the present paper as paralectotype A of the new species) and Johnson (1970, pl. 4, figs 15-19 = ventral, anterior, lateral, posterior, and dorsal views; specimen donated by G.A. Cooper, designated in the present paper as paralectotype B of the new species), respectively, all specimens have been collected by

Sartenaer in May 1959 under the guidance of G. Arthur. Cooper.

Ninety per cent of specimens are single ventral and dorsal valves, most of them still embedded in the rock; 10 per cent, including ten specimens from Houghtaling's Glen, are articulated. All specimens are internal moulds, few of them with shell preserved in the umbonal region.

Types, locus typicus, and stratum typicum. Holotype, IRScNB (Royal Belgian Institute of Natural Sciences, Brussels) a12808 (Pl. 2, Figs Ee-Ii). Paratypes C, IRScNBa12809 (Pl. 2, Figs Z-Dd), D, IRScNBa12810 (Pl.2, Figs U-Y), E, IRScNBa 12811 (Pl. 2, Figs P-T), K, IRScNBa 12817 (Pl. 2, Figs K-O), G, IRScNBa12813 (Pl. 2, Figs F-J), H, IRScNBa12814 (Pl. 2, Figs A-E), J, IRScNBa12816 (Fig. 3), F, IRScNBa12812, I, IRScNB12815. Collected by P. Sartenaer, May 1959, under the guidance of G. Arthur Cooper. Paratype A, USNM89866 = pl. 57, fig. 6 in Cooper & Williams, 1935. Paratype B, USNM157320 = pl. 4, figs 15-19 in Johnson, 1970. All types from the Laurens Member of the Tully Formation at Houghtaling's Glen, 1½ mi NE of Laurens, Otsego County, New York.

Diagnosis. The long-standing incorporation of *Eumetabolotoechia alaura* n. sp. in *Katabuporhynchus mesacostalis* is the only justification for comparing the two species that cannot in any way be mistaken for one another.

It must be considered as a comparison between the false Tully "*mesacostalis*" and the true *Ithaca mesacostalis*. The true *mesacostalis* is the specimen N°67, 1a in Hall, 1843, the only one fitting the original description, limited to the nature and number of median costae ("four to six strong ribs along the mesial elevation and depression of either valve, while they become obsolete towards the margins"), and matching the name given to the species. Important features of the species were added to this description by Hall in 1860 ("lateral portions of the shell smooth, or with obscure ribs", "characterized by ...plain or obscurely marked lateral portions of the shell", p. 86) and in 1867 ("more or less gibbous", "shell oval or ovate", "mesial fold and sinus... marked by plications...dichotomous in their upper part", pp. 362-363).

The two species have the following characters in common: maximum thickness not located at front margin, but posterior to it; a short hinge line; commissures sharp; cardinal commissure sticking out; anterior commissure (crest of tongue) slightly serrate; top of tongue located lower than maximum shell thickness; a moderate number of low and rounded costae; irregular median costae due to divisions and intercalations, start at or very near to the beaks; simple lateral costae; shell thick posteriorly; teeth short, small, simple; septum slender; dental sockets short, shallow; crural bases well marked; and, a ventral field narrow and elongated.

Katabuporhynchus mesacostalis can be separated from *Eumetabolotoechia alaura* n. sp. by a larger size; a transversely oval to elliptical outline (longitudinally ovate in *E. alaura*);

inflated umbonal regions; maximum width located around mid-length (anterior to mid-length in *E. alaura*); a wider apical angle; sulcus and fold starting at or very close to the beaks; a deeper sulcus; a higher fold; a higher tongue; the absence of parietal costae; the absence of lateral costae in the majority of specimens; when present, lateral costae are shorter, in fewer number, and evanescent at various distances from beaks; dental plates very short, sometimes vestigial (absent in *E. alaura* n. sp.); teeth dorsally directed (dorsally-internally directed in *E. alaura* n. sp.); a thick hinge plate (no actual hinge plate in *E. alaura* n. sp.); a very shallow median depression in the hinge plate (a crural trough in *E. alaura* n. sp.); and, short crura, rounded to suboval in section, only slightly curved ventrally at their distal end (long, crescent-shaped in distal section with ends curving ventrally in *E. alaura* n. sp.).

Description. Shell of medium size. Profile lens-shaped, valves of subequal thickness, and slightly convex. Outline longitudinally ovate, sometimes asymmetrical, exceptionally tending to become subcircular. Hinge line short. Cardinal commissure sticking out as a result of postero-lateral margins of shell becoming concave near the commissure; anterior and lateral commissures sharp; anterior commissure very slightly serrate, lateral commissures almost smooth. Very shallow sulcus and very low fold well marked, start in the umbonal regions, mostly near to the beaks. Length is larger than width, and much larger than thickness. Dorsal and ventral valves thickest anterior to posterior of mid-length (36 to 60 per cent anterior to ventral beak), and posterior to mid-length (27 to 44 per cent anterior to ventral beak), respectively, gently sloping from these points towards front margin. Maximum width around and anterior to mid-length (46 to 72 per cent anterior to ventral beak). Apical angle moderately to very wide, variable. Ventral beak wide, slightly (generally) to strongly incurved. Ventral interarea short (20 to 39 per cent of shell width), defined by faint ridges. Sulcus stretched anteriorly, extended dorsally as a very low tongue with trapezoidal outline; bottom of sulcus slightly convex; width of sulcus at front ranging from narrow to wide. Crest of tongue flat, located considerably lower (20 to 35 per cent) than maximum shell thickness. Costae in moderate number, very low, flat-rounded; median costae often divided or intercalated, and thus irregular, start near to the beaks, may be even at the beaks where they usually are obsolete; lateral costae simple, evanescent posteriorly; external lateral costae usually mere undulations of the commissure (counting of lateral costae is affected by poor preservation on molds); parietal costae often present (one on one side or on either side, exceptionally two on one side), and internal ventral lateral costae usually slightly higher than the others. The general costal formula is: $6to7/5to6$; 0; 6 to 13. The number of median costae counted on 54 specimens is as follows: 4/3 : 2 sp. (3.5%); 5/4 : 9 sp. (16.5%); 6/5 : 28 sp. (52%); 7/6 : 14 sp. (26%); 8/7 : 1 sp. (2%).

Shell thick posteriorly. Dental plates absent in two specimens that have been serial sectioned. Dental sockets short, narrow. Teeth short, simple, cyrtomatodont, dorsally-internally directed.

in mm	Paratype C IRScNBa 12809	Holotype IRScNBa 12808	Paratype D IRScNBa 12810	Paratype E IRScNBa 12811	Paratype J IRScNBa 12816	Paratype F IRScNBa 12812	Paratype K IRScNBa 12817	Paratype G IRScNBa 12813	Paratype H IRScNBa 12814	Paratype I IRScNBa 12815
l	22.9	22.1	22.2	21.7	22.5	21.5	22.4	18	17.3	12.5
lvv unrolled	28	29	26	26	30	25	28.2	25.5	21	15
w	23.9	22.3	(22.2)	20.9	20.4	20.1	20	17.9	16.4	11.7
t	11.8	13.1	11.3	10.2	14.4	10.1	12.2	14.2	9.2	6.2
tvv	5	6	5.6	4.2	6.1	4.9	5.8	6.1	4.5	3.1
tdv	6.8	7.1	5.7	6	8.3	5.2	6.4	8.1	4.7	3.1
l/w	0.96	0.99	(1)	1.04	1.10	1.07	1.12	1.01	1.05	1.07
t/w	0.49	0.59	(0.51)	0.49	0.71	0.50	0.61	0.79	0.56	0.53
t/l	0.52	0.59	0.51	0.47	0.64	0.47	0.54	0.79	0.53	0.50
Apical angle	128°	115°	119°	(120°)	98°	(115°)	(107°)	112°	110°	94°

Table 1. Measurements of ten specimens of *Eumetabolotoechia alaura* n. sp; figures in parentheses estimates. Abbreviations: l = length; w = width; t = thickness; vv = ventral valve; dv = dorsal valve.

Septum thick posteriorly, growing thinner anteriorly, reach almost mid-length. Septalium small (narrow and moderately deep to deep), better described as a crural trough. No actual hinge plate; instead depressions separated from the crural trough by two well-marked projections. Inner socket ridges robust, only slightly higher than hinge plate. Crural bases stout. Crura long, raduliform, rounded in proximal section, crescent-shaped in distal section, and with ends curving ventrally. Ventral muscle field slightly impressed, narrow, elongate (netting needle-shaped), not reaching further than the posterior third of shell length.

Measurements of ten specimens, of which seven have been photographed, and one serially sectioned (paratype J), are given on Table 1.

Discussion. *Eumetabolotoechia laura* and *E. alaura* n. sp. have many external features in common, e.g. a longitudinally ovate outline, a short hinge line, the location of maximum thickness of both valves, a moderate number of costae, and irregular median costae due to divisions and intercalations.

E. laura can easily be separated from *E. alaura* by its larger size, greater thickness of both valves, and thus dorsal flanks sloping abruptly towards the antero-lateral commissures, generally strongly incurved ventral beak in contact with the inflated dorsal umbonal region, higher fold, deeper sulcus, higher tongue, stronger, wider, and higher median costae, fewer and usually better marked lateral costae, and a more deeply serrated anterior commissure.

This comparison is based on more than one hundred specimens of *E. laura* from the *stratum typicum* (Hungry Hollow and lower Widder formations, Middle *Polygnathus varcus* Zone) and type area between Arkona to the south and Thedford (Ausable River; Bosanquet = *locus typicus*) to the north in south-western Ontario, Canada.

Range and distribution. The stratigraphic range of *Eumetabolotoechia alaura* n. sp. is that of the Tully “*mesacostalis*”. When Cooper (1933, p. 541 as *Leiorhynchus mesacostale*) mentioned *mesacostalis* as characterizing the *Leiorhynchus* zone or the *Hypothyridina-Leiorhynchus* beds of the Tully Formation in eastern New York, he was probably influenced by Hall’s figure (1843, fig. N°67, 1b) as the figure presented by Cooper & Williams (1935, pl.57, fig. 16) indicates. Cooper (1934, pp. 3, 6 as *L. mesacostale*) restricted the presence of the species to the base of the Tully Formation, precisely to the Laurens Member of that formation, and proposed a *Hypothyridina-Leiorhynchus mesacostale* zone. Cooper & Williams (1935, pp. 807, 809, 810, 812, 814, 815, 816, 818, 822, 856) extended the range of the species to a new member, the New Lisbon Member, proposed for the *Leiorhynchus* beds extending from the top of the Hamilton to the first appearance of *Hypothyridina* (now *Tullypothyridina*). Further east, they gave the following stratigraphic range for the species: Unadilla Formation, 50 feet above the *Vitula* (now *Pustulatia*) bed of the Hamilton Formation in the Unadilla Valley; first *Hypothyridina* zone (= lowest of the three zones recognized in the Laurens Member that contains abundant *Tullypothyridina*) in the Otego Valley; lower half of the Tully Formation in the Susquehanna Valley; and, Tully Formation, 30 feet above top of Hamilton, and Gilboa Formation (quarry dump) in the Schenevus Valley.

Since then the presence of *mesacostalis* in the lower part of the Tully Formation gained wide acceptance by various authors as demonstrated by a few examples: Stevenson & Skinner (1949, p. 30 as *Leiorhynchus mesacostale*); Cooper [1967, p. 702 as *Camarotoechia* (formerly *Leiorhynchus*)]; Johnson (1970, pp. 2082, 2083 as *L. mesacostale* of the Tully, and explanation of pl. 4, figs 15-19, p. 2100 as *L. cf. mesacostale*); Heckel (1973, p. 10, fig. 4, p. 11, pp. 56-57, 130, 142 as *L. mesacostale*, and p. 142 as *Leiorhynchus*-bearing strata); Kirchgasser et al. [1985, table, p. 248 as *L. (?) mesacostale* Beds of Cooper & Williams, 1935]. Baird (1998, p. A-40 as *L.? mesocostale* and *L.? mesocostale*-dominated fauna); Baird & Brett [2003, pp. 146, 150, fig. 7, p. 151 as *Camarotoechia* (“*Leiorhynchus*”) *mesacostale*]; Brett et al. (2007, p. 321 as *Leiorhynchus mesacostale*); and, Baird & Brett [2008, fig. 3, p. 361 as *Camarotoechia* (“*Leiorhynchus*”)

mesocostale, and pp. 362, 364, fig. 5, p. 365, fig. 6, p. 367 as *Camarotoechia mesocostale*].

In short, *Eumetabolotoechia alaura* n. sp. is restricted to the Lower Tully Formation (New Lisbon and Laurens members). The presence of the species in the Upper Tully Formation mentioned in the literature is discussed below.

The geographic distribution of *E. alaura* n. sp. is the one given by Cooper & Williams (1935, pp. 807, 809, 811, 812, 814, 815, 816, 818, foot-note 19 as *Leiorhynchus mesacostale*) in east-central New York, i.e. in the following valleys from west to east: Chenango Valley, Unadilla Valley (New Berlin, Pittsfield, also as *Leiorhynchus* beds), Butternut Valley (Stony Creek, also as *Leiorhynchus* beds), Otego Valley (Houghtaling’s Glen, 1½ mi north-east of Laurens), Susquehanna Valley (east of Milford), and Schenevus Valley (Schenevus), upper part of Summit Hill (quarry dump).

A *Eumetabolotoechia alaura* Zone is proposed. The geographic distribution of *Eumetabolotoechia alaura* is to the east of the one of *Katabuporhynchus mesacostalis*.

Is *Eumetabolotoechia alaura* n. sp. present in Pennsylvania? In other words is the Pennsylvanian *mesacostalis* the same species (or a closely related species) as the central New York *mesacostalis* (the Tully “*mesacostalis*”) that is renamed *E. alaura* n. sp. in the present paper?

Willard (1935b, pp. 1203, 1210, 1212, fig. 2, p. 1213, p. 1214) mentioned at the base of the Trimmers Rock sandstone at Brodhead Creek north of Stroudsburg (Monroe County, EC Pennsylvania) a faunule with *Hypothyridina*, *Liorhynchus mesacostale*, and *Echinocoelia*; this faunule, associated with Ithaca fossils, was considered by him as related to the fauna of the Laurens Member of the Tully Formation at its type locality in EC New York [Remark: this “faunal zone” was already mentioned by Willard (1935a, p. 41) without *Liorhynchus mesacostale*]. Willard (1937, pp. 1244-1245, table 1, p. 1247) confirmed that *Liorhynchus mesacostale*, *Hypothyridina venustula* and *Echinocoelia ambocoelioides*, “specifically identified” at the base of the Trimmers Rock (“Ithaca”) sandstone at Brodhead Creek (also spelled Broadhead Creek and Brodheads Creek) occurred “in the Laurens”. Willard (1939, table XXV, p. 239, p. 231) repeated that the “association of *Liorhynchus mesacostale*, *Hypothyridina venustula* and *Echinocoelia ambocoelioides*” at Brodhead Creek (also spelled Brodheads Creek) was “suggestive of the Laurens”.

The species has since been mentioned by various authors, e.g. in the Weissport and Brodhead members, the basal and middle members of the Tully clastics, by Stevenson & Skinner (1949, pp. 30, 31, 33), who also cited the Brodhead locality and wrote: “*Leiorhynchus mesacostale* dominated the fauna at the beginning of Tully clastic deposition”; and by Heckel (1969, p. 14 as *L. mesocostale*) in the Weissport Member of the Tully Formation.

Mesacostalis is certainly not to be found in the detrital Tully equivalent of east-central Pennsylvania, considered as corresponding to the detrital Tully equivalent of east-central New York, i. e. the Weissport and Brodhead members considered as corresponding to the New Lisbon and Laurens members, respectively.

No specimen has been spotted in the collections examined by the author, who was told by Dr. Heckel, Philip H. in Iowa City on August 31, 1981 that he did not collect any specimen, and that mentions of the species in his publications were taken from the literature.

Proposal of an Eumetabolotoechia Zone. An Upper Givetian (Middle *Polygnathus varcus* Zone) North American *Eumetabolotoechia* Zone is proposed with incorporation of the following species: *E. laura* (type species; Hungry Hollow and lower Widder formation, southwestern Ontario), *E. alaura* n. sp. (*E. alaura* Zone, Lower Tully Formation, east-central New York); *E. greeni* Cleland, 1911 (Milwaukee Formation, south-central Wisconsin; assigned to the genus *Eumetabolotoechia* in the present paper), *E. huronensis* Nicholson, 1874 (upper Widder Formation, southwestern Ontario), and *E. kelloggi* (Silica Formation, northwest Ohio; Plum Brook Formation, north-central Ohio).

Presence of mesacostalis outside the Lower Tully and Ithaca Formations. *Mesacostalis* has been mentioned almost at any

stratigraphic level from the Upper Givetian to the Famennian, including among the variously defined Portage, Naples, and Chemung faunas: Moscow Formation (Windom, Gage Gully), Upper Tully Formation, Genesee Group (Genesee, Lodi, Penn Yan, North Evans, Sherburne, Cornell), Sonyea Group (Middlesex), West Falls Group (Rhinestreet, Java, Nunda), Canadaway Group, Conneaut Group, and Conewango Group (Catarauqua, Venango).

What are these so-named *mesacostalis*, below the Tully “*mesacostalis*” (now *Eumetabolotoechia alaura* Zone), between this zone and the *mesacostalis* (now *Katabuporhynchus mesacostalis* Zone), and above it?

Most of them are citations without descriptions or/and illustrations. Large collections with precise stratigraphic information are needed in order to properly characterize the various taxa that will have to be considered. The author has no such collections. The present paper, thus, represents only a piece of the puzzle, and is intended to encourage regional geologists and brachiopod specialists to build on it.

It would not take too much effort to properly identify the *mesacostalis* collected from well known localities and stratigraphic units, such as those from the Lower Carpenter Falls, Smyrna, and Taughannock Falls beds, i.e. from the top of the Lower Tully and the lower part of the Upper Tully, mentioned by Baird & Brett (2003 fig. 7, pp. 150-151; 2008, fig. 3, p. 361, p. 368) or those of “Ithaca type” mentioned by Cooper & Williams (1935, fig. 3, p. 803, p. 805) and having their “first appearance” in the Sherburne Formation of the Otselic, Chenango and Unadilla valleys.

3. Acknowledgements

This paper would not have been possible without the assistance of many people. Data for this study are based on large collections examined in the American Museum of Natural History in New York (AMNH), the National Museum of Natural History in Washington (NMNH), Cornell University at Ithaca, the British Museum of Natural History in London (BMNH), and other scientific institutions. Samples were collected under the expert guidance in the field of the late Drs John W. Wells (Cornell University) and G. Arthur Cooper (NMNH). The author will never forget that, when he was a Postdoctoral Fellow of the Belgian American Educational Foundation at Yale University, he was introduced to the geology of the Devonian of southwestern and central New York by the late Dr Carl O Dunbar, who spent two weeks with him in the field. Access to the collections under their charge was allowed by the late Dr Norman D. Newell (AMNH), the late Dr G. Arthur Cooper, and Fred Collier (NMNH), the late Dr John W Wells (Cornell University), and the late Dr C. Howard Brunton and Dr Sarah Long (BMNH). In July 1975 the author had the privilege to examine in the Paleontological Museum of Cornell University the specimens of *mesacostalis* collected by Jonathan W. Harrington in connection with his PhD (1968).

The late Dr Norman D. Newell is particularly acknowledged for the extended loan of types and permission to photograph them. Critical comment on the manuscript, suggestions for improvement, additional information, and linguistic assistance by Drs Carlton E. Brett (University of Cincinnati, Ohio) and William T. Kirchgasser (State University of New York at Potsdam, USA) were much appreciated.

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Appendix

Mentions of the species outside central New York, with some reservation about EC Pennsylvania, are not valid. This can be easily ascertained when figures have been published and/or when collections are available. Otherwise, mere mentions in the literature are synonym of incorrect identifications; some have already been corrected, others will have to be progressively ironed out. The following list is in no way extensive.

North America

Alberta

Kindle (1928, pp. 16, 17 as *Leiorhynchus mesacostale*), Lower Portage equivalent, Peace River; Norris in Norris & Uyeno (1983, p. 3 as *L. mesacostale*, referring to Kindle, 1928), Lower Frasnian (now Upper Givetian), Gypsum Cliffs area on Peace River, NE Alberta. This species from the Firebag Member (Lowermost *Polygnathus asymmetricus* Zone) of the lower Waterways Formation is known as *L. russelli* McLaren, 1962, a species that has been designated by Sartenaer (1970, pp. 1, 2) the type species of the genus *Platyterorhynchus* Sartenaer, 1970.

Arkansas

Girty (1909, pp. 26-27, pl. II, figs 11, 12 as *Liorhynchus* aff. *mesicostale*), Moorefield shale (Upper Mississippian), NE Arkansas, redefined as *L. carboniferum* by Girty (1911, pp. 57-58).

Kentucky

Campbell (1946, pp. 861, 863, 864 as *Leiorhynchus* cf. *L. mesacostale*), Portwood Formation (Middle Givetian), EC Kentucky; Brett et al. (2009, pp. 25, 28, 33 as *L. mesacostale* and *Camarotoechia mesacostale*, referring to Campbell), middle interval of the Portwood Member of the Ohio Shale or New Albany Formation, C. Kentucky.

Maryland

Prosser in Prosser & Swartz (1913, pp. 364, 367, 369), Swartz in Prosser & Swartz (1913, pp. 411, 415-416, table, p. 440, pp. 474, 517, 518, 526-527), and Clarke & Swartz (1913, p. 581, pl. LIV, figs 5-8) as *Liorhynchus mesacostalis* and *L. mesacostalis* zone, Parkhead Member of Jennings Formation (Frasnian), Parkhead, Washington County, near Cumberland, western slope of Polish Mountain, near Allegany Groove, various outcrops along the National Road, notably west of Tonoloway Ridge; Amsden (1951, table, p. 99, p. 122 as *Leiorhynchus mesacostale*), Parkhead Member of Jennings Formation, Washington County; Swartz (1958, pl. X, figs 25, 26 as *L. mesacostale* = pl. LIV, figs 5, 6 in Clarke & Swartz, 1913).

Montana

Raymond (1907, p. 119, table, p. 121 as *Leiorhynchus mesicostale*?; 1909, p. 142, pl. III, figs 8, 9 as *L. mesacostale*), zones 1, 2, 4, and 5 near Three Forks, and zone 4 at Logan, Gallatin County, SW Montana; zones 1 to 5, from base to top, are subdivisions of the Three Forks shales of highest Devonian age. Haynes (1916, table, p. 25, pp. 39, 42 as *L. mesacostale* and *L. mesacostale*?), member 5 in the northern part of the Three Forks quadrangle; members 1 to 7, from base to top, are subdivisions of the Three Forks Formation. Holland (1952, p. 1706 as *Nudirostra mesicostale*), uppermost exposed limestone bed in the Three Forks at Sappington type section. Crickmay (1952, p. 588 as *Leiorhynchus mesacostale*?; referring to Haynes and Holland), upper limestone bed and associated shale at Three Forks. Warren & Stelck (1956, pl. XXV, figs 4, 5 as *N. mesacostalis* = pl. III, figs 8, 9 in Raymond, 1909), *Platyclymenia* fauna. All mentions of the species are from the Middle Famennian.

Nevada

Johnson (1970, pp. 2077, 2085, table 1, p. 2087, pp. 2100, 2102 *pro parte*, pl. 1, figs 16-20 as *Leiorhynchus. mesacostale*, *L. aff. mesacostale*, *L.* of the *mesacostale* type, and small *L. sp.* related

to *L. mesacostale* of the Tully), Denay Limestone (Couvianian-Givetian), Willow Creek, northern Roberts Mountains; Johnson (1977, p. 25, table 5, p. 27 as “*L.*” cf. *mesacostale* and “*L.*” of the *mesacostale* type), Intervals 20, 21 (middle subzone of the *varcus* Zone). Johnson (1978, p. 126) realized that an “association with *Camarotoechia mesacostale*” seemed “no longer tenable”, and proposed a new species, *C. vesper*, as a substitute for his previous identifications.

New Mexico

Flower (1965, p. 119; 1969, p. 39 as *L. cf. mesacostalis*), Thoroughgood Formation (Middle Famennian), San Andres Mountains; Bowsher (1967, p. 261 as *L. mesacostale*), latest Middle Devonian, Sacramento and San Andres Mountains; Johnson (1970, pp. 2077, 2082, 2100, 2102 *pro parte* as *L. mesacostale*, *L.* of the *mesacostale* type, and small *L. sp.* related to *L. mesacostale* of the Tully), Oñate Formation (Upper Givetian), Sacramento Mountains. The Thoroughgood species has been put by Sartenaer (1987a, p. 85) into the synonymy of *Insignitiusinurostrum latisinuatum* (Cooper & Dutro, 1982).

Ohio

Newberry (1873, pp. 164, 166-167, 190, 197, 488 as *Leiorhynchus. mesacostalis*), Erie shale (upper Portage + Chemung), various counties (Ashtabula, Cugahoga, and Lake); Prosser (1912, pp. 80, 81, 82, 84, 113, 114, 117, 118, 181, 188, 247, 282, 285, 286, 436, 437, 438, 439, 444, 456, 457, 459, list p. 463, pp. 533, 534, 545, 546 as *Liorhynchus mesicostale*, *L. mesicostale*?, *Leiorhynchus mesacostalis* (when referring to Newberry) and *L. mesacostalis* = *Liorhynchus mesicostale*), Chagrin shale (formerly Erie shale), same counties; Chadwick (1934, p. 351 as *L. mesacostale*), Chagrin shale (Famennian); and Hoover (1960, appendix, p. 139 as *L. mesicostale*?), Chagrin shale. These identifications stand probably for *L. ohioense* Prosser, 1912 and/or *L. clarkei* Prosser, 1912 as suggested by Prosser (1912, p. 533) and Clarke in Prosser (1912, pp. 545-546), respectively.

Oklahoma

Girty (1909, pp. 26-27, pl. II, figs 11, 12 as *Liorhynchus* aff. *mesicostale*), Caney shale (Lower Mississippian), Atoka quadrangle, redefined as *L. carboniferum* by Girty (1911, pp. 24, 54, 57-58, 60).

Ontario

Savage & Van Tuyl (1919, p. 373 as *Leiorhynchus* aff. *mesacostalis*), Abitibi River limestone (Frasnian), Abitibi River; Dyer (1929, p. 28 as *L. aff. mesacostalis*), Williams Island Formation (“mixture of Upper and Middle Devonian”), Williams Island; Martison (1953, p. 44 as *L. cf. mesacostale*, reported by Savage and Van Tuyl, Williams Island Formation “correlatable with the upper part of the Hamilton or with the Tully” according to Dyer); Fritz et al. [1957, p. 25 as *L. sp.* (aff. *mesacostatus*)], probably Givetian, Williams Island; Sanford & Norris (1975, p. 68 as *L. aff. mesacostalis*), Williams Island Formation (Upper Givetian or Lower Frasnian). Norris in Norris et al. (1992, p. 43) believes that *Calvinaria* sp. cf. *ambigua* (Calvin, 1878) could be the appropriate name for this Ontario species.

Pennsylvania

See text.

West Virginia

Kindle in Williams & Kindle (1905, pp. 37, 38) and Williams in Williams & Kindle (1905, chart between p. 54 and p. 55, as *L. mesicostale*, Chemung, near Sulphur Springs); Price et al. (1938, p. 184, pl. 102, fig. 3 as *Liorhynchus mesacostalis* and *L. mesacostale*), Portage Series.

Outside of North America

Algeria

Flamand (1911, pp. 163, 166, 176, 212) and Borghi (1939, pp. 128, 129, 154) as *Leiorhynchus mesacostalis*, near Ben Zireg (Famennian), and Ougarta (Saoura area), NW Algeria (Upper Devonian).

Belgium

Beugnies et al. (1962, p. 204 as *L. mesacostalis*), Lower Famennian, Leval-Chaudeville (Dinant Synclinorium).

Libya

Massa & Collomb (1960, p. 71) and Freulon (1964, pp. 99, 100 as *L. mesacostalis*), Aouinet Ouenine Formation (Frasnian), Aouinet Ouenine area (Fezzan).

Maroc

Massa et al. (1965, p. 106, Table, pp. 154-155 as *Leiorhynchus* cf. *mesacostalis*), Famennian (probably Lower Famennian), Jbel Amelane (Tafilalt).

Niger

Barrere & Slansky (1965, p. 31 as *Leiorhynchus* sp. eg. *mesacostale*), base of the Middle Devonian, Djado area; de Lestang (1968, p. 483 as *Leiorhynchus* sp. gr. *mesocostale*), Upper Givetian or Frasnian, Djado (west flank); Fabre et al. (2005, p. 280 as *L. eg. mesacostalis*), Upper Givetian or transition Givetian/Frasnian, Djado Basin.

Poland

Sobolev (1909, pp. 117, 122, table, p. 308, table, p. 324, table, p. 358, pp. 501-502, table, p. 533 as *Liorhynchus* aff. *mesacostalis* and *L. aff. mesacostalis*?; two varieties), lower and upper *Stringocephalus* beds, Holy Cross Mountains (Kielce-Sandomir area).

Russia

Kuznetsk Basin. Rzhonsnitskaya (1953, p. 173, table, p. 179, pl. X, fig. 8 as *Liorhynchus* cf. *mesacostalis*, Lower Frasnian; 1978, p. 179, table between p. 184 and p. 185, p. 189 as *Leiorhynchus* cf. *mesacostalis*, Lower Frasnian).

Novaya Zemlya. Nalivkin (1947, p. 16 as *Liorhynchus mesacostalis*), Frasnian.

Ural Mountains. It would be of no use to give a list of some hundred publications in which *mesacostalis* has been mentioned from the Ural Mountains in the Russian literature. Chernyshev (1887, pp. 91-92, table between p. 124 and p. 125, pp. 130, 131, 188, 189, pl. XIV, figs 3a-d, 4a-d as *Rhynchonella mesacostalis*) described the species in the *Spirifer Anosofi* and *Stringocephalus Burtini* horizon of the western flank of the Ural Mountains. Since then, the species has been mentioned from the Eifelian to the Middle Famennian under various names (*Liorhynchus mesocostalis*, *L. cf. mesacostalis*, *L. aff. mesacostalis*, *Leiorhynchus mesacostalis*, *L. cf. mesacostalis*, *L. (?) ex gr. mesacostalis*) in many localities along the Urals chain, from the Mugodjary Mountains to the south to the Polar Urals to the north.

Timan. Nefedova (1955, p. 424, table 2, p. 450 as *Liorhynchus* aff. *mesacostalis*, Lower Frasnian, and as *L. mesacostalis*, Middle Frasnian).

The misconception of the genus *Leiorhynchus* and of *mesacostalis* in Russia is best illustrated in Rozman's publication (1962, pp. 76, 106-107). She divided the genus into two branches: one including "species with numerous dichotomized costae covering almost the whole surface of the shell", with *L. multicosta* as the typical representative, and including ten species from the Eifelian to the Tournaisian; and the other, including "species with a small number of costae usually only developed in the sulcus and on the fold, and poorly developed or absent on the flanks; sometimes there are no costae at all", with *L. mesacostalis* as the typical representative, and including twelve species from the Famennian to the Lower Carboniferous. The first branch incorporates three New York species, *limitaris*, *multicosta*, and *quadricostata*, also present in the Givetian (Urals), the Middle Frasnian (Volga-Urals region), and Frasnian (Urals and Volga-Urals region). The second branch incorporates an Ohio species, *kelloggi*, also present in the Givetian (Urals), two New York species, *mesacostalis* considered of Famennian age, and *globuliforme* from the Chemung, and a southern Indiana species, *greenianum* (Ulrich, 1886) considered of Lower Carboniferous age.

Tchad

de Lestang (1968, p. 483 as *Leiorhynchus* sp. gr. *mesocostale*), Bidejat Formation (Upper Givetian or Frasnian), Borku-Ennedi, NE Tchad.

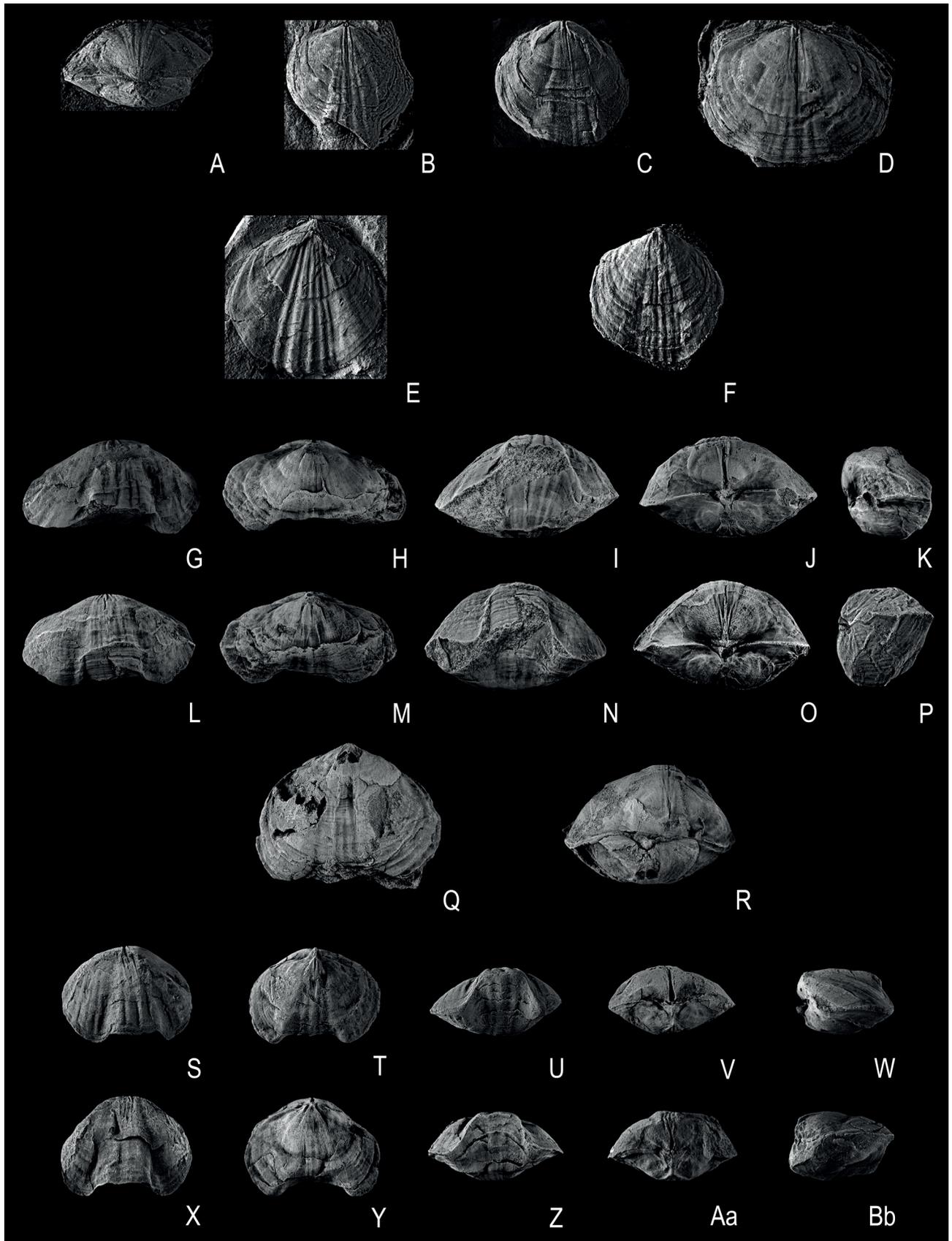


Plate 1: *Katabuporhynchus mesacostalis* (Hall, 1843); all figures are natural size. A : Lectotype, AMNH-FI30627; posterior view = fig. 67, 1a, p. 60 in Hall, 1843 as *Atrypa esacostalis* = fig. 1a, p. 86 in Hall, 1860 as *Leiorhynchus mesacostalis* = pl. 57, fig. 20 in Hall, 1867 as *L. mesacostalis*; Chemung group, near Ithaca, New York. B: AMNH-FI37640; dorsal valve = pl. 57, fig. 21 in Hall, 1867; Chemung group, Cortland, New York. C: AMNH-FI37638; dorsal valve = pl. 57, fig. 22 in Hall, 1867; Chemung group, near Ithaca, New York. D: AMNH-FI31682; dorsal valve = pl. 57, fig. 23 in Hall, 1867; Chemung group, Cortland, New York. E: AMNH-FI37642; ventral valve = pl. 57, fig. 24 in Hall, 1867; Chemung group, Chenango County?, New York. F: AMNH-FI31681; ventral valve = pl. 57, fig. 25 in Hall, 1867; Chemung group, Cortland, New York. G-K: IRScNBa12802; dorsal, ventral, anterior, posterior, and lateral views; Cascadilla Creek, Ithaca, New York, Lower Middle Ithaca Formation; collected by P. Sartenaer, October 1967, under the guidance of John W. Wells. L-P: IRScNBa12803; dorsal, ventral, anterior, posterior, and lateral views; same formation, locality, and collector. Q-R: IRScNBa12804; ventral, and posterior views; same formation, locality, and collector. S-W: IRScNBa12805; dorsal, ventral, anterior, posterior, and lateral views; Fall Creek, 3 mi west of Cortland, New York; collected by P. Sartenaer, May 1967, under the guidance of John W. Wells; Costal formula: 3/2; 0; ?. X-Bb: IRScNBa12806; dorsal, ventral, anterior, posterior, and lateral views; same formation locality, and collector; costal formula: 4/3; 0; 4+.

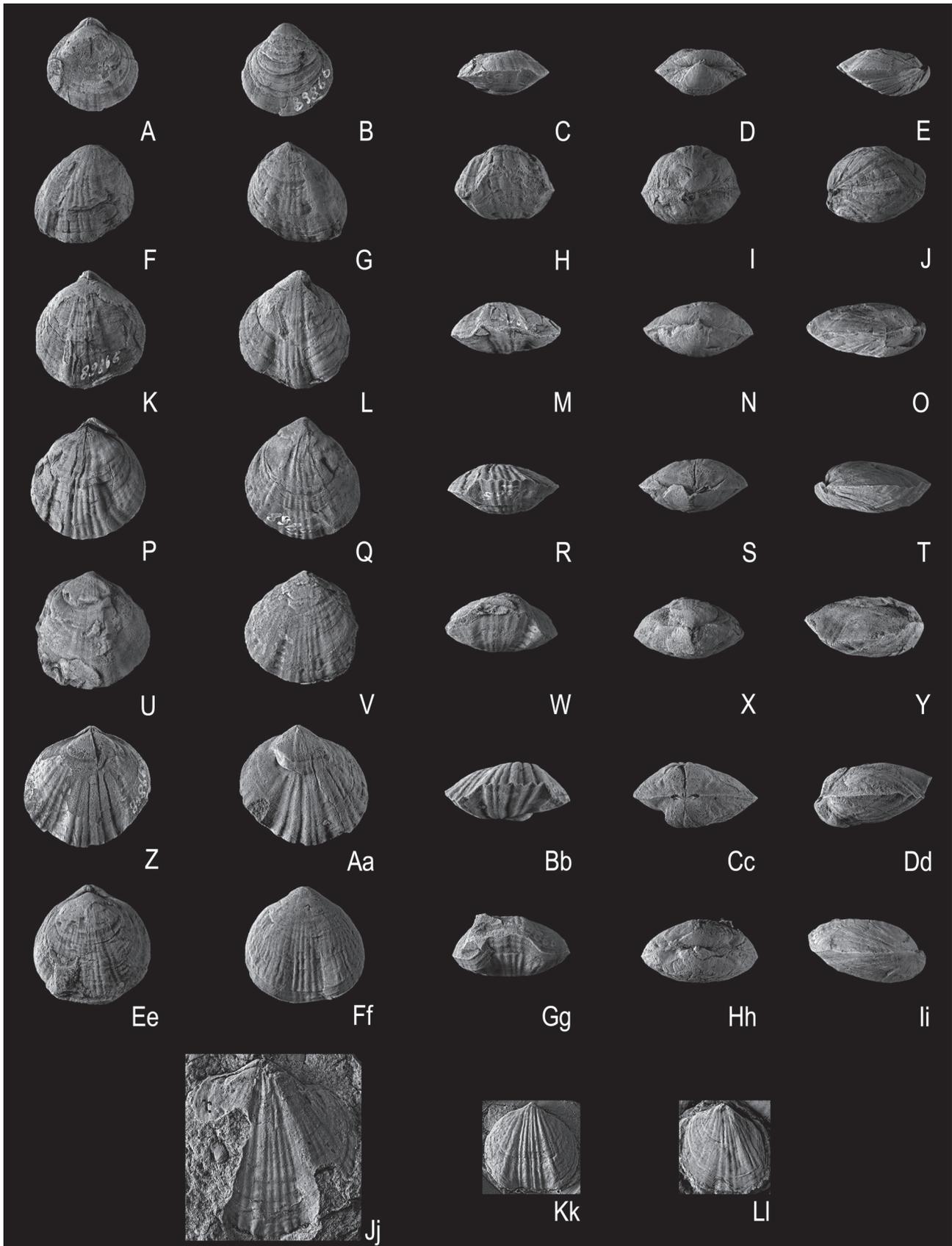


Plate 2: *Eumetabolotoechia alaura* n. sp. All figures are natural size. All specimens come from the Laurens Member of the Tully Formation at Houghtaling's Glen, 1½ mi NE of Laurens, Otsego County, New York. A-E: Paratype H, IRScNBa12814; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 4/3; 0; ?. F-J: Paratype G, IRScNBa12813; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 5/4; 1-1/1-1; 5/6. K-O: Paratype K, IRScNBa12817; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 6/5; 0; 5+/? . P-T: Paratype E, IRScNBa12811; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 7/6; 1-0/1-0; 7+/? . U-Y: Paratype D, IRScNBa12810; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 7/6; 0; 8/6. Z-Dd: Paratype C, IRScNBa12809; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 7/6; 0; 5+. Ee-Ii: Holotype, IRScNBa12808; dorsal, ventral, anterior, posterior, and lateral views; costal formula: 5/4; 1-1/1-1; 10/11.

Incertae sedis. Jj: Paralectotype A, AMNH-FI30627; ventral valve = fig. 67,1, p. 60 in Hall, 1843 as *Atrypa mesacostalis* = fig. 1, p. 86 in Hall, 1860 as *Leiorhynchus mesacostalis*. Chemung group, Fall Creek, near Ithaca, New York. Kk: Paralectotype B, AMNH-FI37639; ventral valve = fig. 67,1b, p. 60 in Hall, 1843 as *Atrypa mesacostalis* = fig. 1b, p. 86 in Hall, 1860 as *Leiorhynchus mesacostalis* = probably pl. 57, fig. 19 in Hall, 1867 as *L. mesacostalis*; Chemung group, south part of Steuben County, New York. Ll: AMNH-FI 6041/1; ventral valve = pl. 57, fig. 18 in Hall, 1867 as *Leiorhynchus mesacostalis*; Chemung group, near Ithaca, New York.