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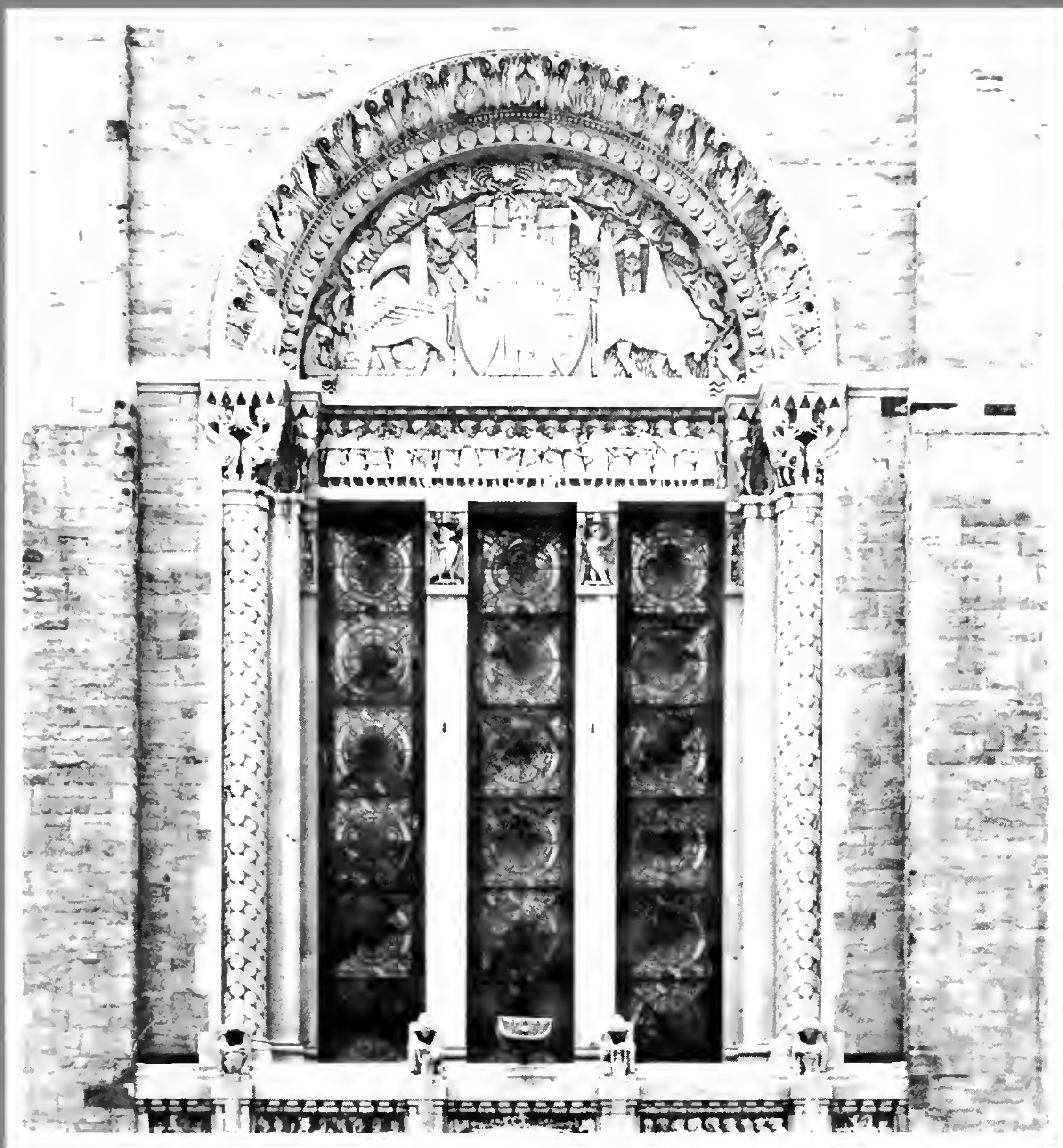

The Type Species of the Ordovician Trilobite Genus *Isotelus: I. gigas* Dekay, 1824

David M. Rudkin and Ronald P. Tripp

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The Type Species of the Ordovician Trilobite Genus *Isotelus: I. gigas* Dekay, 1824

Abstract

In 1824 Dekay erected the genus *Isotelus* with *gigas* as first named species; the type locality is the Trenton Falls gorge, New York State, United States. A neotype is selected from a collection made by Walcott in the Denley Formation (late Shermanian), in an excavation adjacent to the gorge. *Isotelus gigas* and an associated species, *I. walcotti* Walcott, are redescribed with emphasis on the range in dimensions. Material from the lower Verulam Formation (early Shermanian), Ontario, Canada, is identical with topotype *I. gigas*. The prosopon of the librigena is a distinctive character.

Introduction

Isotelus was one of the first trilobites to be described from the New World; it is also one of the largest and most abundant trilobites in Ordovician rocks. Dekay (1824:174), in his original description of *Isotelus gigas,* states only that the specimens he described were found by Mr. John Sherman of Olden Barneveld at Trenton Falls. Dekay recognized them as belonging to a new genus, for which he proposed the name *Isotelus* (from the Greek, equal extremities). He also briefly described a smaller specimen as a second species, *I. planus,* remarking, "This may possibly prove the young of the preceding species," a view with which we agree.

The Trenton Falls gorge of West Canada Creek exposes approximately 80 m of Trenton Group strata (Kay, 1953:26), including the type sections, in ascending order, of the Poland, Russia, and Rust members (Kay, 1943) of the Denley Formation (Kay, 1968:1377); Titus (1986) does not recognize these members. Williams and Telford (1986) equate the Denley Formation with the late Shermanian Stage. White (1896) and Raymond (1903) documented that *Isotelus* (identified by both as *Asaphus platycephalus*) occurs throughout the exposure. The precise horizon from which Dekay's type material originated cannot be determined with certainty. However, all the *Isotelus* material from Trenton Falls that we have seen is attributable to the two species described herein. Access to the Trenton Falls gorge is now restricted by the Niagara Mohawk Power Corporation.

Materials and Methods

Between 1871 and 1873 C. D. Walcott and others made a large collection in a ravine 1 km east of Sherman Fall, from beds 8.23 m below the top of the Denley Formation (Text-fig. 1). The Walcott Collection from this locality (now in the Museum of Comparative Zoology, Harvard University) is remarkable for the great number of carefully developed dorsal shields of *Isotelus* that it contains. It provides the only adequate sample from a single horizon near West Canada Creek (Trenton Falls), and the descriptions in the present paper are based largely on this collection. As neotype, we select the dorsal shield figured by Raymond in 1914 and Whittington in 1950.

Terminology and abbreviations used in this paper are essentially those of Harrington, Moore, and Stubblefield (1959:117–126). The term *eye socle* (Shaw and Ormiston, 1964) is applied to the raised but concave part of the librigena, which is continuous with the lens surface in *Isotelus gigas*. *Dorsal shield* is the term used for specimens exposing the cephalon, thorax, and pygidium—and occasionally part of the doublure. The term *terrace ridge* is applied to positive linear sculptural elements with conspicuous cross-sectional asymmetry, that is, with a shallow slope and a steep face. The closely spaced parallel ridges and striae on the bevelled inner slope of the forks of the hypostome are referred to as *corrugations*. Miller (1975) presented a general discussion of terrace morphology.

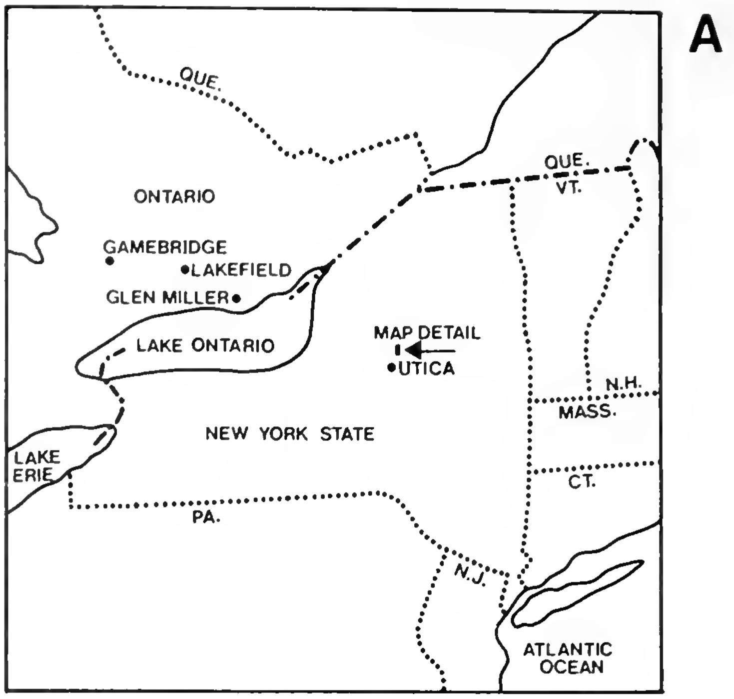
Additional morphological terms and dimensions are shown on Text-figure 2. Up to 15 variables, which are listed below, were measured for each of the 56 most complete specimens available. Variables used in the calculation of shape indices have a letter designation and are shown schematically on Text-figure 3. Shape indices are simple dimensional ratios expressed as percentages; the most useful of these are summarized on Text-figure 3.

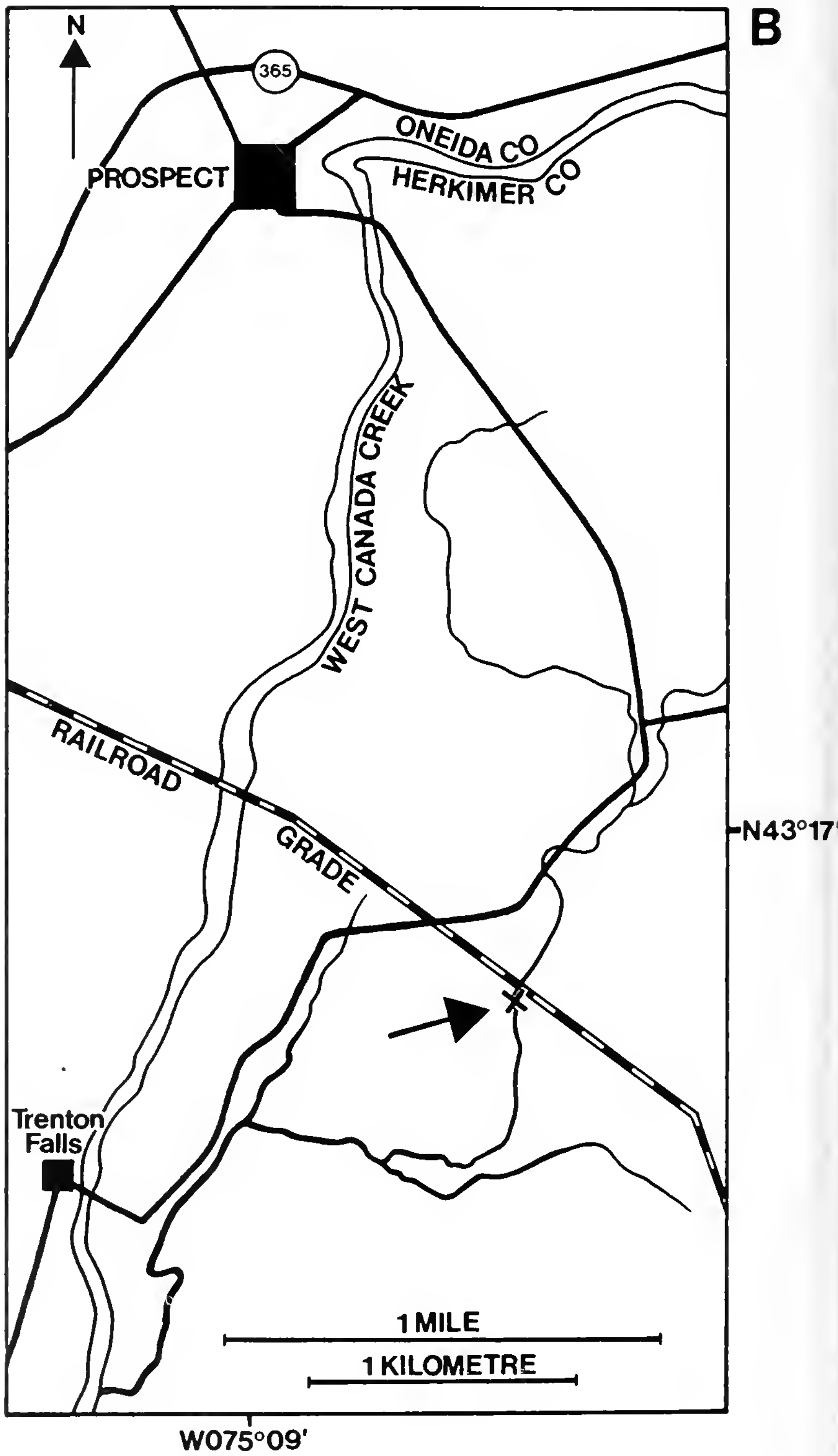
length of dorsal shield B
length of cranidium D
length of thorax
length of pygidium E
length of pygidial axis
length of cranidium to minimum width H
width of cephalon A
minimum width between eyes C
maximum preocular width of cranidium G
maximum palpebral width
basal width of glabella between apodemes
maximum width of cranidium at posterior margin
width of thorax
maximum width of pygidium F
number of thoracic segment to which genal spine extends

All measurements in the text are given in millimetres (mm). A complete list of measurements is available from the authors upon request.

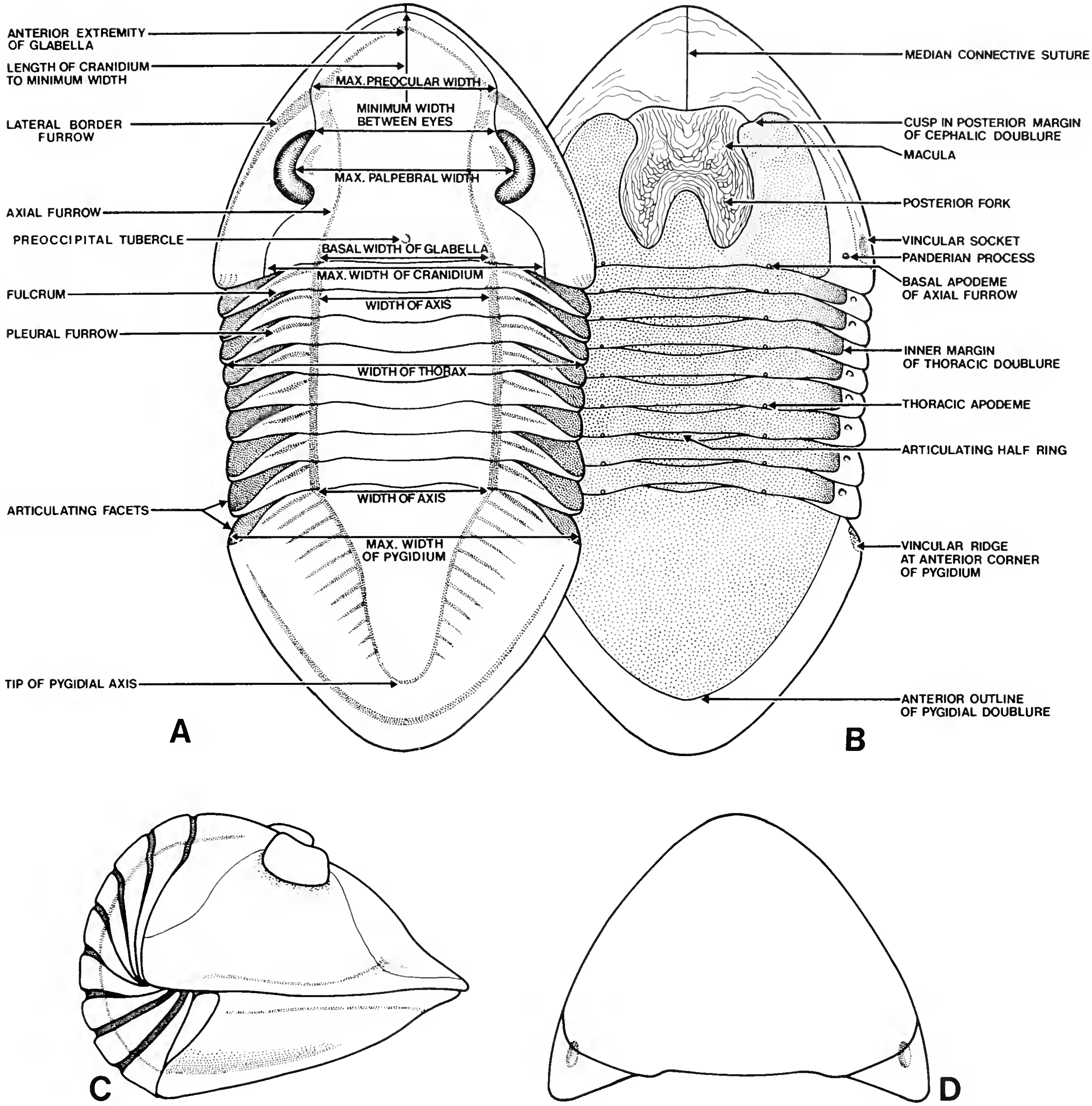
Specimens figured herein were lightly coated with ammonium chloride before being photographed. All but the one shown in Figure 2.3 are testiferous; Figure 2.3 is a photograph of a latex cast taken from an external mould.

Specimens studied are deposited in the following institutions: British Museum (Natural History), London (BMNH); Buffalo Museum of Science (BMS); Field Museum of Natural History, Chicago (UC); Geological Survey of Canada, Ottawa (GSC); Museum of Comparative Zoology, Harvard University, Cambridge (HMCZ); New York State Museum, Albany (NYSM); Royal Ontario Museum, Toronto (ROM); National Museum of Natural History, Washington, D.C. (USNM).

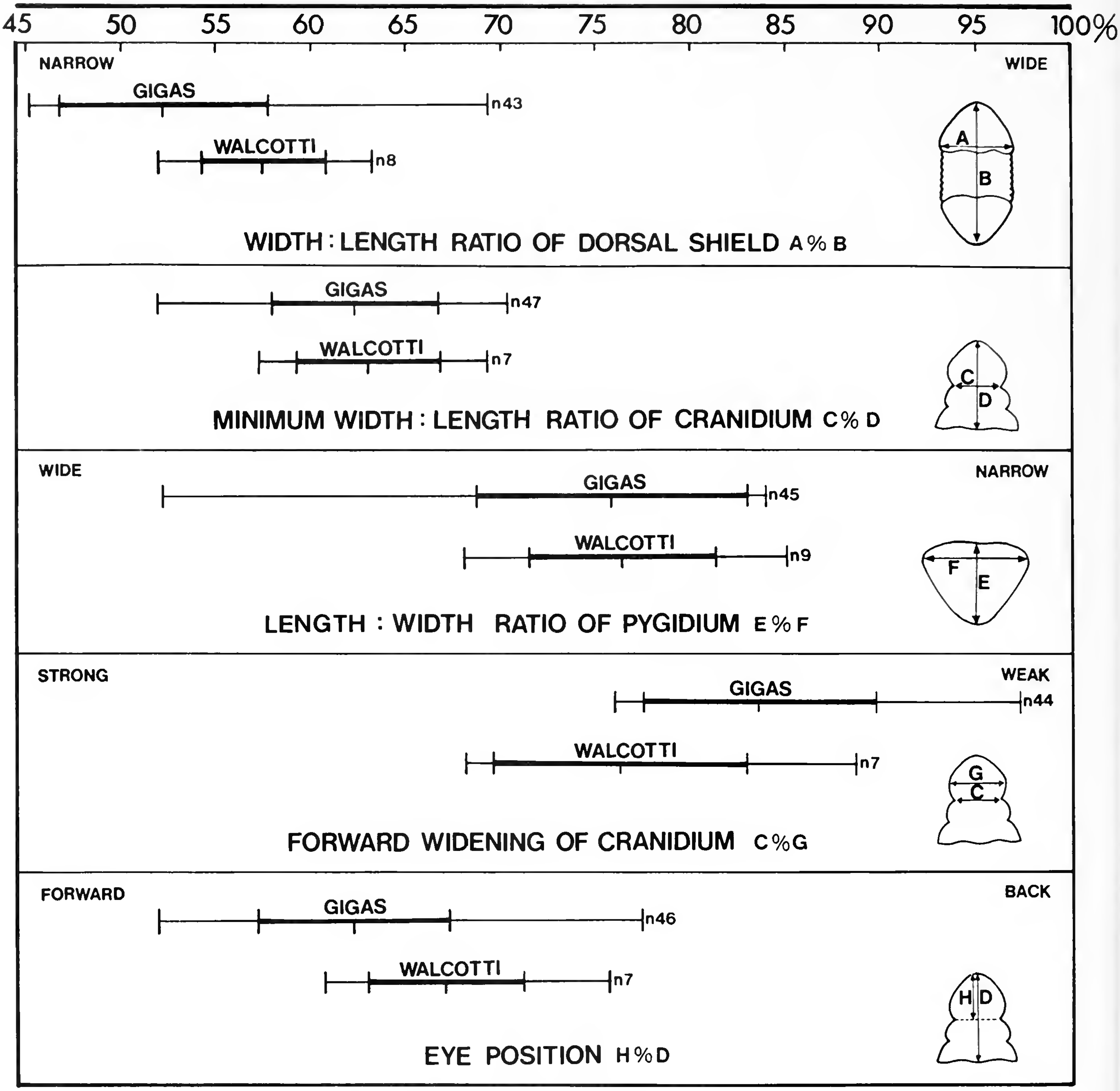




TEXT-FIG. 1. *A*, Outline map showing localities in New York and Ontario yielding specimens of *Isotelus* illustrated in this paper. *B*, Map detail from *A* showing position of the Walcott excavation (arrow and X). Trenton Falls gorge extends south from below the bend in West Canada Creek at Prospect to immediately north of Trenton Falls village.



TEXT-FIG. 2. Schematic drawings of *Isotelus gigas* Dekay. *A,B*, Dorsal and ventral views showing major morphological terms used in this paper. *C*, Enrolled individual, right lateral view showing position of tips of the seventh and eighth thoracic pleurae beneath the cephalic doublure. *D*, Outline of cephalon and pygidium showing position of genal vincular sockets relative to anterolateral corners of pygidium.



Text-Fig. 3. Comparison of significant shape indices for *Isotelus gigas* and *I. walcotti* in Walcott Collection (HMCZ). Ratios are expressed as percentages. Thin line denotes range; thick line denotes one Standard Deviation around mean.

Systematic Palaeontology

Family Asaphidae Burmeister, 1843
Subfamily Isotelinae Angelin, 1854
Genus *Isotelus* Dekay, 1824

Note: Balashova (1976:66) elevated the subfamily Isotelinae Angelin to familial status. We prefer to retain the usage of Jaanusson (1959:339) and treat the taxon as a subfamily.

TYPE SPECIES

Isotelus gigas Dekay (selected Bassler, 1915:675), Trenton Falls, New York State, United States.

DISCUSSION

Schmidt (1901:86) wrote "Im Nachstehenden fassen wir unter dem Gattungsnamen *Isotelus* zwei Gruppen zusammen. Den Typischen auf *I. gigas* gestützen *Isotelus* von Dekay und die von Salter (British Trilobites p. 196) 1866 aufgestellte Untergattung *Brachyaspis*, die sich auf *Asaphus rectifrons* Portl. ..." We regard Schmidt's comment as a factual statement that Dekay based his genus *Isotelus* on *I. gigas*, and not as an indication that Schmidt deliberately selected *I. gigas* as type species for the genus.

In the following synonymy we include only references to specimens that we believe to be conspecific with the topotype sample of *I. gigas*, as defined below.

Isotelus gigas Dekay, 1824

Figs. 1.1–6; 2.1–3; 3.1–12; Text-fig. 2

Isotelus gigas Dekay, 1824:176, pl. 12, figs. 1,2; pl. 13, fig. 1.
Isotelus planus Dekay, 1824:178, pl. 13, fig. 2.
Isotelus Megalops [*sic*] Green, 1832a:70, cast 25.
Giant isotelus (Isotelus gigas) [*sic*] Vanuxem, 1842:47, fig. 1.
Isotelus gigas—Hall, 1847:231, pl. 63, fig. 1.
Isotelus sp. Raymond and Narraway, 1910:56, pl. 15, fig. 3.
Isotelus gigas—Raymond, 1910a, fig. 1.
Isotelus gigas—Raymond, 1914:248, pl. 1, figs. 1,2; pl. 2, figs. 2–5; pl. 3, fig. 3.
Isotelus gigas—Bassler, 1919, pl. 48, figs. 23–25.
Isotelus gigas—Raymond, 1920:91, fig. 28.
Isotelus gigas—Foerste, 1924:241, pl. 44, fig. 6.
Isotelus gigas—Whittington, 1950, pl. 73, figs. 1,2,4.
Isotelus gigas—Howell, 1951:265, pl. 2, fig. 3.
Isotelus gigas—Jaanusson, 1959, figs. 251,2a,b.
Isotelus gigas—Whittington, 1960, fig. 4b.
Isotelus—Whittington, 1961:17.
Isotelus—Whittington, 1962, pl. 8.
Isotelus gigas—Lu et al., 1965:123, pl. 28, figs. 2a,b (as Jaanusson, 1959).
Isotelus gigas—Darby and Stumm, 1965, pl. 1, fig. 7.
Isotelus gigas—Henningsmoen, 1975, fig. 13.
Isotelus gigas—Towe, 1973:1008, figs. 1f,g,k,l.
Isotelus gigas—Levi-Setti, 1975, pl. 55.
Isotelus gigas—Teigler and Towe, 1975, pl. 1, figs. 1,2; pl. 2, fig. 2; pl. 3, figs. 2,5; pl. 7, figs. 1,2.
Isotelus gigas—Ludvigsen, 1978, pl. 1, figs. 18,19 [non fig. 17].
Isotelus gigas—Ludvigsen, 1979a, figs. 24c,d.
Isotelus gigas—Ludvigsen, 1979b, figs. 6G,H, 12E–H.

DIAGNOSIS

Cephalon and pygidium with lateral border furrow strongly developed as a broad depression. Posterior border of fixigenae undefined. Anterior branches of facial sutures diverging weakly forward. Librigenal spines absent in dorsal shields more than 60 mm in sagittal length. Axial furrows of pygidium not impressed. Cephalon coarsely pitted; terrace ridges on border of cephalon and pygidium, and on eye socle.

NEOTYPE

Hereby selected HMCZ 41 (extended testiferous dorsal shield, Walcott Collection, figured Raymond, 1914, pl. 3, fig. 3; Whittington, 1950, pl. 73, figs. 1,2,4; Jaanusson, 1959, fig. 251,2a; Lu et al., 1965, pl. 28, figs. 2a,b; Ludvigsen, 1979b, fig. 12H; this paper, Figs. 1.1–3, 2.1,2); from a horizon 8.23 m below top of the Denley Formation (late Shermanian), Walcott's excavation in a ravine 1 km east of Sherman Fall, West Canada Creek, Herkimer County, New York State, United States. The exact locality was established by Dr. Ellis Yochelson (pers. comm.), by reference to a deed issued by Mr. W. P. Rust leasing Walcott digging rights on this site.

No specimen studied by Dekay is known. A poorly preserved plaster cast in the New York State Museum, Albany (NYSM 4510), is labelled "taken from the original of Dekay's pl. 13, fig. 1; specimen does not match figure very well." The breadth of the head of this cast is 2.8 inches, which is to be compared with 3.5 inches quoted by Dekay for the specimen in question; the thoracic segments are telescoped, not extended as in Dekay's illustration, and there is little general similarity. It may be the cast of one of Dekay's syntypes, but it is quite inadequate to stand as the type specimen of the type species of *Isotelus*.

TOPOTYPE MATERIAL

HMCZ (Walcott Collection): Forty-one well-preserved dorsal shields, most fully extended; three enrolled dorsal shields; numerous exoskeletal parts and hypostomes. Walcott affixed green labels bearing the number 50 to the back of many specimens from his excavation. The specimens of *Ceraurus* with appendages, which he first described in 1877, are from the same locality. Walcott (1875:155) recorded that the horizon was "about 27 feet below the coarse crystalline limestone that caps the upper portion of the ravine," referring in all likelihood to a bed high in the Rust Member and just beneath the Steuben Member, as subsequently defined by Kay (1943:601). The excavation came to be known variously as Walcott's Quarry, the Trilobite Quarry, and the Rust Quarry; it is now completely obscured by debris. The fauna was listed by Delo (1934).

USNM (Rust Collection): Six well-preserved, extended dorsal shields, and other parts. Labels bear the locality number 316.

DESCRIPTION

Dorsal shield oval in outline; maximum width across genal angles 45 to 69 per cent sagittal length (Text-fig. 3). Genal spines present in all dorsal shields up to 45 mm in sagittal length (cephala less than 16 mm), present or absent in dorsal shields 45 to 60 mm in length (sag.), absent in larger specimens (cephala more than 20 mm). In dorsal shields up to 100 mm in length (sag.), pygidium usually shorter than cephalon; in all larger specimens, pygidium longer than cephalon. Thorax shorter than either cephalon or pygidium. Dorsal surface characterized by conspicuous shallow circular pits of various sizes up to approximately 200 μm in diameter, which become steadily weaker towards the back of the exoskeleton; pitting variable in strength among specimens. Terrace ridges on border and eye socle.

Cephalon subtriangular to parabolic in outline, moderately convex in both directions, 50 to 70 per cent as long as wide; height about 45 per cent length (sag.) of cranidium and 80 per cent minimum width between eyes. Minimum width of cranidium between eyes 52 to 71 per cent length (sag.) of cranidium, 76 to 97 per cent maximum preocular width; situated at 52 to 77 per cent length from front of cranidium (Text-fig. 3; all ranges based on specimens in Walcott Collection). Glabella completely fused with occipital ring, clearly defined by moderate independent convexity, about 85 per cent length (sag.) of cranidium, narrowing forward to 75 per cent its posterior width opposite anterior extremity of palpebral lobe, and widening to basal width at front. Faint longitudinal keel extending most of length of cranidium on some specimens. Small, inconspicuous preoccipital tubercle present on most specimens, stronger on internal surface. Occipital furrow effaced. First and second lateral lobes and furrows faintly distinguishable on some specimens. Axial furrow distinct and broad posteriorly, convergent and becoming shallower forward, divergent anteriorly, and curving round frontal part of glabella. Distance between basal apodemes 50 to 81 per cent posterior width of cranidium. Anterior margin of glabella subangular, defined by broad preglabellar furrow, which deepens adaxially. Anterior border of cranidium 15 per cent length of cranidium, crescentic, wider adaxially than abaxially, gently convex. Fixigena narrow (tr.) posteriorly, width between sutures at posterior margin 115 to 120 per cent length (sag.) of cranidium. Posterior border and furrow absent. Palpebral lobe 15 to 20 per cent cranidial length; posterior extremities slightly farther apart than anterior; lobe sloping gently forward and inward, slightly saucer-shaped. Anterior branch of facial suture diverging slowly forward from eye to 25 to 35 per cent length (sag.) from front of cranidium, thence curving inward to midpoint intramarginally, giving cranidium a lanceolate appearance anteriorly; sutures joined in even, ogive-shaped curve. Short median connective suture on dorsal surface present or absent. Posterior branch swinging outward and backward at 35 degrees to sagittal axis, cutting posterior margin at 85 per cent width between genal angles. Surface densely pitted, most strongly on front part of glabella; pitting faint on external surface of largest specimens and absent on internal surface. Doublure of dorsally effaced occipital ring comparatively short, narrowing abaxially. Doublure of posterior border absent except for a triangular area abaxially.

Librigena sloping steeply outward. Eye about 25 per cent length (sag.) of cephalon, lens surface holochroal (Walcott, 1877, footnote to p. 95, records 7536 facets in an eye on cephalon 45 mm in length), strongly curved in outline, weakly so in a vertical plane; posterior extremities farther apart (tr.) than anterior. Subocular depression broad and shallow, drawn up to lens surface to form a concave eye socle, not marked off from lens surface. Field moderately convex. Lateral border furrow a broad concave area continuous with preglabellar furrow, broad anteriorly, narrowing with decreasing independent concavity posterior to midlength. Posterior border furrow absent. Both posterior and lateral margins gently rounded. Genal angle subrectangular, or with slender genal spine rising abruptly at genal angle, directed straight backward. Pitting of field of librigena usually coarser than on any other part, and always distinguishable on external moulds. Concentric terrace ridges on eye socle. Lateral border, genal spine, and lateral border furrow bearing numerous delicate anastomosing terrace ridges that run parallel to lateral margin and on some librigenae extend a short distance onto abaxial area of field and show a reticulate pattern here and elsewhere on exoskeleton. Cephalic doublure 40 to 45 per cent cephalic length, horizontal, flattened. Inner margin broadly embayed mesially to accommodate anterior margin of hypostome, extended into a cusp opposite anterior extremity of eye; cusps 35 per cent maximum width of cephalon apart. Doublure narrowing slowly backward from cusp, turning abruptly inward at back to meet lateral doublure of posterior border of cranidium where facial suture cuts posterior margin. Median connective suture sometimes absent or partially fused (Henningsmoen, 1975, fig. 13B). Elongate vincular socket measuring 10 per cent sagittal length of cephalon, placed close to margin of doublure at just over its own length anterior to genal angle. Doublure flattening out and becoming swollen towards and at socket, with flattening dying out immediately behind socket. Panderian opening placed a short distance posterior and adaxial to vincular socket; crescentic anterior rim slightly raised (panderian protuberance). Terrace ridges evenly spaced, running parallel to margin and traversing vincular socket.

Hypostome subquadrate, as long (exsag.) as wide, weakly convex. Anterior margin gently concave forward. Anterior wing trapezoidal, projecting slightly backward and downward. Lateral margin evenly rounded. Middle body defined by independent convexity and shallow posteromedian depression; faint maculae at 30 per cent from front, 50 per cent maximum width of hypostome apart. Median notch extending 45 per cent length (sag.) of hypostome, margin diverging steadily at 20 degrees to midline, apex broadly rounded. Posterior fork narrowing steadily backward, tips 50 per cent maximum width of hypostome apart. Ventral surface of hypostome bearing a few scattered pits. Four or five semicontinuous terrace ridges running parallel to margin abaxially, and subparallel to margin of posteromedian embayment, with steep slopes facing away from margins. Prosopon on median area of forks taking on a reticulate pattern in some specimens. On middle body, adaxial to maculae, terrace ridges arranged in a broadly U-shaped pattern. Anterior margin of doublure transverse for median 45 per cent width, running a short way anterior to apex of notch, curving forward sharply and extending to anterior wing abaxially. Posterior wing process just anterior to bend projecting laterally and dorsally. Doublure beneath fork triangular in cross-section, swollen to form a deep keel curving forward from tip and convex outward, dying out gradually anteriorly; inner slope flat, bevelled, with about 50 closely spaced, straight, parallel corrugations running obliquely, and curving forward near crest of keel; occasional corrugations bifurcating downward. Outer surface convex, with a few widely spaced sinuous terrace ridges running parallel to margin, steep slopes facing outward.

Thorax composed of eight segments, parallel-sided. Anterior width of axis equal to basal width of glabella and 40 to 60 per cent width of thorax, narrowing a little backward, gently convex transversely. Rings weakly convex longitudinally, gently convex backward; faint muscle impressions near midwidth and abaxially. Axial furrow deep and narrow, straight; small apodeme at anterior extremity of each segment. Pleurae subhorizontal adaxially, curved downward and backward at fulcrum near midwidth; pleural furrows strong, oblique, broad (exsag.) adaxially, narrowing abaxially. Articulating facet broad (tr.), narrowing (exsag.) adaxially, extending inward to fulcrum, bearing reticulate terrace ridges that trend parallel to oblique inner margin of facet. Terminations of pleurae truncated and bluntly round. Pitting, restricted largely to axis, becoming weaker on successive segments. Articulating half-ring less than half length (sag.) of ring. Ring furrow broad and shallow; socket at abaxial extremity coaptative with apodeme under posterior margin. Pleural doublure 45 per cent width of pleura, with inner margin running exsagittally for most of length, widening (tr.) abruptly and extending inward to fulcrum at back. Crescentic panderian openings and protuberances placed adaxially and anteriorly to midpoint of doublure. Terrace ridges running subparallel to margin adaxially and abaxially, diverging backward mesially.

Pygidium subtriangular, 52 to 84 per cent as long as wide (Text-fig. 3). Axis 45 per cent anterior width and 64 to 90 per cent length of pygidium, narrowing steadily backward to narrowly rounded apex. Twelve axial rings faintly marked by indistinct ring furrows on surface, clearer on internal moulds. Axis defined only by change in convexity, apex raised. Axial furrow not impressed. Articulating half-ring and furrow short. Anterolateral facet broad (tr.), extending to axial furrow, narrowing (exsag.) adaxially, declined forward at about 60 degrees; terrace ridges as on thoracic facets. Lateral margin of facet projecting slightly ventrally and terminating posteriorly in a vincular ridge, which fits into librigenal ventral vincular socket, together with the extremities of the seventh and eighth segments. First pleural furrow deep and broad, marking off a swollen first half-pleura. Pleural lobe moderately and evenly convex, gently declined. Lateral border furrow shallow, marking off lateral border of uniform width, almost half postaxial length mesially. Eight to ten short pleural ribs faintly but variably developed, dying out just beyond midwidth. Pleural furrows short, successively less well defined towards back. Pitting on pygidium fainter than on cranidium, obliterated on large specimens. Terrace ridges on border oblique for most of length, parallel to margin posteriorly, steep slopes posterolaterally directed. Doublure 20 to 25 per cent length of pygidium at sagittal axis, extending to tip of axis, narrowing forward, anterior margin not embayed mesially; doublure convex and upcurved adaxially with convexity dying out forward, flat abaxially. Seventeen continuous subparallel terrace ridges at midline; first 12 terminating successively farther forward on anterior margin of doublure, posterior terraces terminating at the posterior margin. Terrace ridges only slightly more closely spaced towards front. Single, short terrace ridges intercalated laterally. All terrace ridges on doublure with steep slopes facing outward.

Material from the lower Verulam Formation (early Shermanian), Ontario, Canada (Ludvigsen, 1978, pl. 1, figs. 18,19; 1979a, figs. 24c,d; this paper, Figs. 1.4–6; 2.3; 3.1–6, 9,11,12), is closely similar to the topotype *Isotelus gigas* material and is certainly conspecific. The only significant differences in the Verulam Formation material are that (1) the genal spines are lost at a smaller size in some specimens—the cephalon of a dorsal shield (Figs. 3.11,12) 38 mm in sagittal length lacks spines, whereas the smallest topotype dorsal shield without spines is more than 45 mm in length, and (2) the prosopon is stronger on the librigenae—in some specimens faint terrace ridges are present over the whole field (Fig. 2.3) and the reticulate pattern is more frequently developed. Several cephalic doublures from this unit show that the median connective suture is usually completely fused, but it may be open for a short distance or for the full length, no matter what the size of the individual. In explanation we suggest that when the shell was resorbed as the animal approached a moult, the suture opened up to assist in ecdysis.

A holaspid growth series for *I. gigas* has been well illustrated by Raymond (1914). A small holaspis 9.4 mm in sagittal length is closely similar to full-grown specimens except for the presence of genal spines. In dorsal shields 9 to 22 mm in length, spines extend to the seventh or eighth thoracic segment; in those from 29 to 45 mm, to the fourth or fifth. In spinous dorsal shields from 45 to 60 mm in length, genal spines extend to the second, third, or fourth segment; in this group, three dorsal shields (including the neotype) retain thornlike genal spines, clearly marking the first postspinous moult. Recent collecting from the Verulam Formation at Gamebridge, Glen Miller, Lakefield, and Bolsover, Ontario, yielded 48 pygidia under 25 mm in sagittal length. The smallest pygidium is 5.0 mm in sagittal length and 65 per cent as long as it is wide, with the axis strongly raised and incorporating four protothoracic segments; the posteromedian notch is absent. A slightly larger specimen incorporates two protothoracic segments. Oblique terrace ridges, variable in strength, are present on all specimens. The length:width ratio at a length of 20 mm (sag.) varies from 65 to 95 per cent. With increase in size, the axis becomes less well defined. The surface of the smallest pygidium is smooth; pitting is first present at 14 mm sagittal length.

Whittington's analysis (1957:445, figs. 25–28) of *I. gigas* specimens in the Walcott Collection (HMCZ) revealed a constancy of eye position and virtually rectilinear relationships between width and length of the dorsal shield and lengths and widths of the cephalon and pygidium, through holaspid growth. We restudied the Walcott Collection, and additional material, and reached the same general conclusions (Text-fig. 3).

A few *I. gigas* individuals grew to a great size, though never to a size comparable with that of the holotype of *I. brachycephalus* Foerste (1919), which is 378 mm in length. The largest individual of *I. gigas* that we have recorded is represented by a pygidium, probably from Trenton Falls (NYSM E2690), which is 98 mm in length and had an estimated dorsal shield length of 265 mm.

FUNCTIONAL MORPHOLOGY AND MODE OF LIFE

Isotelus is an effaced, isopygous, flat-lying trilobite lacking an anterior arch. The eyes, which stand high on the cephalon, are elevated in some species. The hypostome is oriented horizontally, with the flat lower surface parallel to the cephalic margins and at a slight angle to the gentle forward slope of the palpebral lobes. This configuration is unlike that described for the bumastoid stance burrower *Symphysurus palpebrosus* (Fortey, 1986). It thus seems highly unlikely that *Isotelus* was an infaunal filter feeder. Ventral appendages in *Isotelus* have been described by a number of authors (Billings, 1870; Walcott, 1881, 1884, 1918; Mickleborough, 1883; Beecher, 1902; Raymond, 1910b, 1920), but all descriptions were based on poorly preserved material. However, what little is known of appendage morphology, combined with evidence from trace fossils (see Osgood, 1970; Seilacher, 1970; Hofmann, 1979), suggests that the adult *Isotelus* had limited capabilities as a swimmer. It probably functioned as an epibenthic or shallow infaunal scavenger/predator, digging subhorizontal furrows and lying covered by a thin layer of sediment, with its eyes exposed.

Isotelus gigas is occasionally preserved in various random orientations relative to the bedding, at or near the type locality. Walcott (1875:158) recorded that "of seventy-five [specimens] noted, thirty were back down, twenty-nine presented the dorsal surface up, sixteen were in various positions, coiled, perpendicular to the layer, and edgeways." It seems probable that this variation is a result of entombment in suspended sediment flows associated with the development of a steep carbonate bank margin during the later stages of deposition of the Denley Formation (Titus, 1986:818, fig. 7).

The external surface of both *I. gigas* and *I. walcotti* is characteristically pitted, never punctate; the internal surface is slightly less strongly pitted. The pitting is usually coarsest on the field of the librigena, strong peripherally on the cranidium, and absent on the border. On the thorax, the pitting is largely restricted to the axis; it becomes steadily weaker towards the back of the dorsal shield and is often hardly distinguishable on the pygidium. The purpose of the pitting is not clear; its strength on the steep slope of the librigenae, and weakness towards the back, suggests that it might have been sensory.

Terrace ridges are present on the border and socle of the librigena; these take on a reticulate pattern in specimens with a prominent prosopon. On the socle, the steep slopes of the concentric terraces face upward. A plausible function of these prosopon elements may have been to stabilize sediment on the near vertical parts of the librigenae, in order to keep the animal partially buried when it was resting. The terrace ridges on the border are oriented with steep faces outward, and it is more difficult to attribute a sediment-stabilizing function to these.

Except for those on the doublure of the thoracic pleurae (see discussion under Enrolment), the function of the terraces on the ventral surfaces remains unresolved. Terrace ridges on the cephalic and pygidial doublure of *I. gigas* have the steep slopes directed outward. Where terraces are present on the ventral surface of the hypostome, they have the steep faces directed more or less sagittally. It is unlikely that the explanation of Schmalfuss (1981) of "sediment gripping" for filter chamber stabilization applies to *Isotelus*. Fortey (1985:229; 1986:273) pointed out many of the difficulties, in general, of accepting a purely sediment-engaging function for terrace ridges.

The corrugated bevelled inner slope of the posterior fork of the *Isotelus* hypostome probably served as a rasping plate to aid in feeding. A similar function has been proposed for the granular subvertical facet on the posteromedian margin of the hypostomes of some odontopleurids (Chatterton and Perry, 1983:16).

ENROLMENT

Adult *Isotelus gigas* dorsal shields are usually preserved more or less extended (41 of the 44 dorsal shields in the Walcott Collection in the HMCZ). In enrolled specimens, margins of cephalon and pygidium fit tightly edge to edge (sphaeroidal enrolment of Bergström [1973:14]; see Raymond, 1912, pl. 2, fig. 7). This tight fit, along with the overlapping of the articulating facets on the thoracic segments, enclosed the animal within the dorsal shield. In fully enrolled specimens, the tips of the seventh thoracic segment locked against the posterior slopes of the vincular sockets in the cephalic doublure, with the tips of the eighth segment in front and the vincular ridges at the anterolateral corners of the pygidial doublure towards the front of the sockets.

The assessment by Fortey (1986:265, fig. 6) of the function of terrace ridges on the petaloid thoracic facet and doublure of *Symphysurus palpebrosus* could apply equally well to *I. gigas*. With full enrolment, the more or less perpendicular orientation of ridges on the opposing facet and doublure would serve to allow passage of sufficient water to permit continued respiration.

In dorsal shields more than 90 mm in length, the sagittal length of the pygidium varies from 100 to 125 per cent of the length of the cranidium. The relative positions of the vincular structures being fixed, the variability in the lengths of cranidia to pygidia was compensated for, during enrolment, mainly by the amount of sweepback in the anterior outline of the pygidium.

DISCUSSION

In 1824 Dekay named, in addition to *Isotelus gigas*, a smaller specimen from Trenton Falls, *I. planus*, stating the length to be 2.1 inches (= 53 mm). His illustration of an extended individual, without genal spines (pl. 13, fig. 2), closely resembles his figure of *I. gigas* on the same plate (fig. 1), except that in *I. planus* the eyes are more forwardly placed (at 43 per cent the length of the cranidium from the front, compared with 55 per cent in *I. gigas*), and the pitting is not shown. Judging from the illustration, we consider *I. planus* to be a junior subjective synonym of *I. gigas*.

As to Green's plaster casts, the locality of the original of cast no. 25 (*I. megalops*) is Trenton Falls, and the specimen may well have been conspecific with *I. gigas* as defined above. Green stated (1832a:69, fig. 7) that his cast no. 24, *I. cyclops* (Green, 1832b), was from a specimen in the Albany Museum, which had been found in an ash-coloured limestone in the western part of New York State. There is no trace of the specimen in the NYSM, and it is doubtful whether it is attributable to *I. gigas*. Green states that the original(s) of his casts nos. 21 and 22 (*I. gigas*) were found near Cincinnati; neither resembles *I. gigas*. Nor does Green's cast no. 23, attributed to *I. planus*, resemble *I. gigas;* the original was recorded as having been found near Newport, Kentucky.

COMPARISON WITH RELATED SPECIES

We have limited the present descriptions to collections from Trenton Falls, New York State, United States, and the lower Verulam of the Province of Ontario, Canada. *Isotelus gigas* is closely related to *I. walcotti;* the degree of similarity is discussed below. Among species with a lateral border furrow and border, the closest relationship of *I. gigas* is to *I. platycephalus* (Stokes, 1824) from the Gull River Formation (Blackriveran), St. Joseph's Island, Lake Huron, Canada, particularly in the coarse pitting of the cephalon. *I. gigas* differs in that (1) the dorsal outline is more angular, (2) the axis of the pygidium is marked only by independent convexity—the axial furrows are not impressed, (3) the anterior margin of the pygidial doublure is unembayed, and (4) the posterior terrace ridges of the pygidial doublure are subparallel, not splayed as in *I. platycephalus*.

Isotelus sp. of Dean (1979) from the Lourdes Limestone (Blackriveran), Newfoundland, also resembles *I. gigas* in many respects—pitted surface, terrace ridges on the border, and eye position. It differs, however, in the sculpture of the hypostome, in which the terraces bend inward at right angles behind the middle body more strongly than in topotype material.

Isotelus walcotti Walcott, 1918

Figs. 1.7–9; 3.13,14

Isotelus iowensis Owen, Raymond, 1914, pl. 2, fig. 6; pl. 3, figs. 1,2.
Isotelus walcotti Ulrich, Walcott, 1918:133 (footnote), pl. 24, fig. 1.
Isotelus walcotti Walcott, Raymond, 1925:98.
Isotelus iowensis—Wilson, 1947, pl. 4 [non pl. 3, fig. 4].

DIAGNOSIS

Differs from *Isotelus gigas* mainly in that genal spines are longer and stouter and extend at least as far as sixth segment in all known specimens—estimated length of largest dorsal shield 127 mm. Convexity is weaker, and cranidium widens more strongly forward on average (Text-fig. 3).

HOLOTYPE

By monotypy, USNM 61261a (extended dorsal shield, figured Walcott, 1918, pl. 24, fig. 1; this paper, Figs. 1.8,9); from a horizon 8.23 m below the top of the Denley Formation (late Shermanian), Walcott's excavation in a ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York State, United States.

TOPOTYPE MATERIAL

USNM: Two dorsal shields.
HMCZ: Seven dorsal shields.
NYSM: One dorsal shield.

DESCRIPTION

Lesser differences are as follows: (1) dorsal shield wider and eyes more backwardly placed, on average (Text-fig. 3), (2) preoccipital tubercle absent, (3) posterior borders of fixigenae faintly marked, (4) palpebral lobes sloping inward more strongly, (5) pitting finer and more subdued, and (6) terrace ridges fainter and never reticulate on librigenae, but much stronger on genal spines. In other features the description of *Isotelus gigas* applies to *I. walcotti* as well.

DISCUSSION

The name *walcotti* was proposed by E. O. Ulrich on labels in the USNM; we follow Raymond (1925:98) in attributing the species to Walcott, 1918. The prime diagnostic characters of *Isotelus walcotti* are the greater width and length of the genal spines in dorsal shields of all sizes and the retention of spines in dorsal shields exceeding 60 mm in length, the size at which spines are lost in *I. gigas*.

Raymond (1914) rightly recognized the resemblance between *I. walcotti* and *I. iowensis* Owen (1852), which ranges from the Platteville Limestone to the Maquoketa Formation, and we figure the holotype dorsal shield for comparison (Fig. 1.10); Darby and Stumm (1965, pl. 1, fig. 6) illustrated a cranidium from the Platteville Limestone near Guttenberg, Iowa. The main resemblances to *I. walcotti* are that both species have the posterior borders of the fixigenae defined and retain genal spines throughout life. *I. walcotti* differs in (1) the weakly defined glabella, (2) the less distinct glabellar lobation, (3) the height of the palpebral lobes (not preserved on the holotype of *I. iowensis* but elevated—tall with a level summit), (4) the stronger genal spines, (5) the undefined pygidial axis (defined by impressed axial furrows in *I. iowensis*), and (6) the prosopon—pitting is denser, and the terrace ridges on the pygidium extend less far inward.

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Figures

Fig. 1. *Isotelus gigas* Dekay, *Isotelus walcotti* Walcott, *Isotelus iowensis* Owen

1.1–3. *Isotelus gigas* Dekay from the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. Neotype HMCZ 41, dorsal shield, × 2.

1. Dorsal view.
2. Right lateral view.
3. Anterior view.

1.4–6. *Isotelus gigas* Dekay from the lower Verulam Formation (early Shermanian), abandoned quarry 1.6 km east of Lakefield, Douro Township, Ontario. GSC 83054, dorsal shield, × 0.5.

4. Right lateral view.
5. Dorsal view.
6. Anterior view.

1.7–9. *Isotelus walcotti* Walcott from the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York.

7. Dorsal shield, right lateral view of cephalon showing genal spine. NYSM 15058, × 2.4.
8. Dorsal shield, oblique right lateral view. Holotype USNM 61261a, × 3.5.
9. Dorsal shield, dorsal view. Holotype USNM 61261a, × 3.2.

1.10. *Isotelus iowensis* Owen from the "lower Maquoketa," mouth of Otter Creek, Turkey River, Iowa. Holotype UC 6308 (Gurley Collection), dorsal shield, × 1.1.

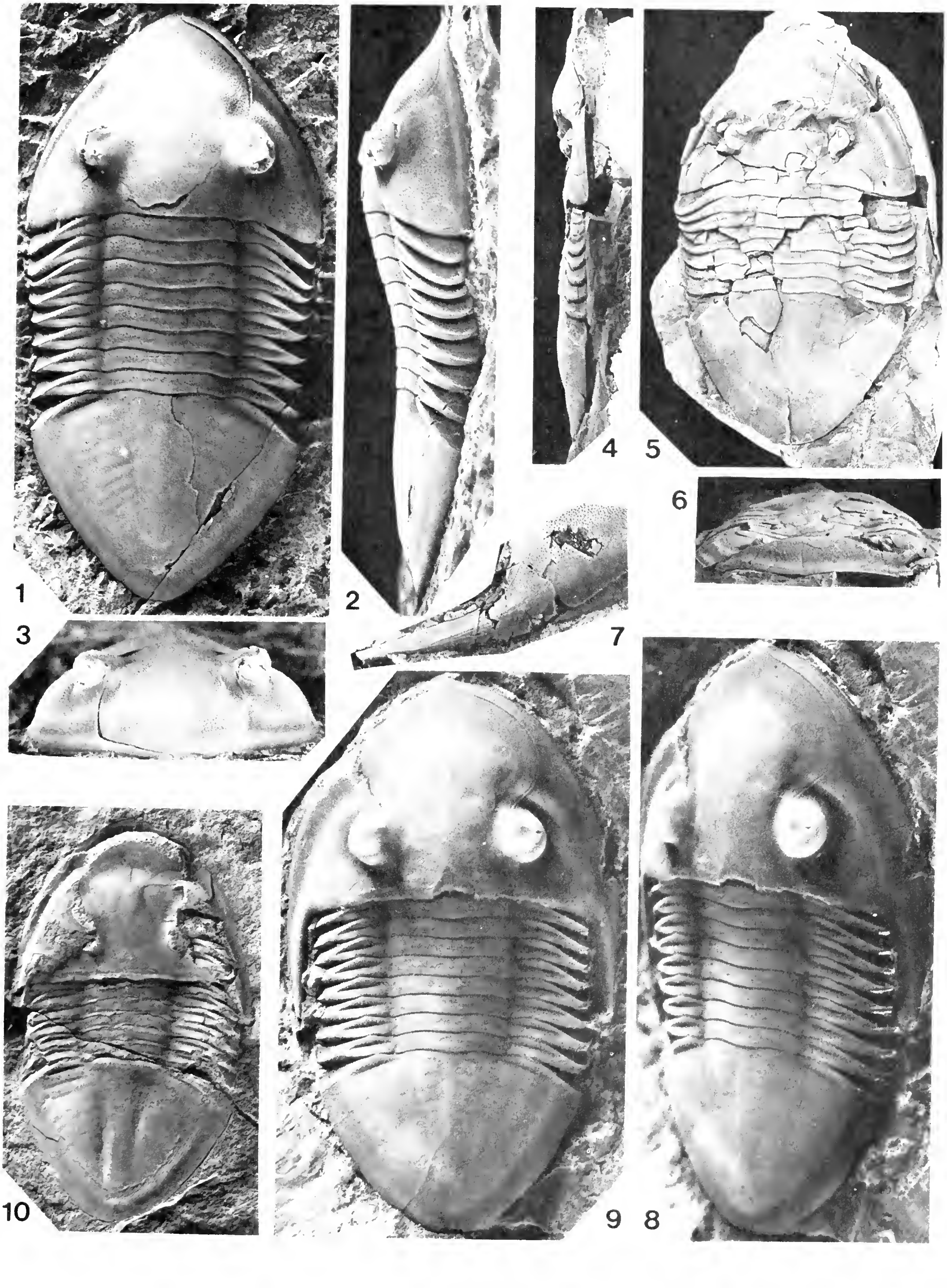
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FIG. 2. *Isotelus gigas* Dekay

2.1,2. *Isotelus gigas* Dekay from the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. Neotype HMCZ 41, dorsal shield, × 7.5.

1. Eye and adaxial area of right librigena.
2. Left librigena.

2.3. *Isotelus gigas* Dekay from the lower Verulam Formation (early Shermanian), Mara Limestone Quarry, Gamebridge, Mara Township, Ontario. ROM 45219, latex cast of external mould of right librigena, × 11.

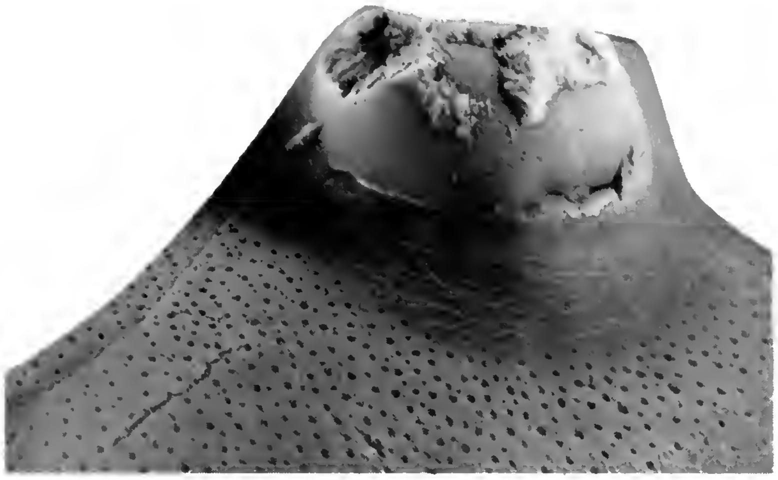

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FIG. 3. *Isotelus gigas* Dekay, *Isotelus walcotti* Walcott

3.1–12. *Isotelus gigas* Dekay.

1. Doublure of cephalon, with complete open median suture, from the lower Verulam Formation (early Shermanian), Mara Limestone Quarry, Gamebridge, Mara Township, Ontario. ROM 45124, × 2.

2. Doublure of cephalon, with short open median suture, from the lower Verulam Formation (early Shermanian), Mara Limestone Quarry, Gamebridge, Mara Township, Ontario. ROM 45220, × 2.

3. Doublure of cephalon, median suture fused, from the lower Verulam Formation (early Shermanian), abandoned quarry 3.2 km south of Lakefield, Douro Township, Ontario. ROM 45123, × 2.

4. Cephalon, left lateral view to show genal spine, from the lower Verulam Formation (early Shermanian), abandoned quarry 1.6 km east of Lakefield, Douro Township, Ontario. ROM 41519, × 2.8.

5. Ventral view of doublure of cephalon (median suture fused) and hypostome, from the lower Verulam Formation (early Shermanian), abandoned quarry 1.6 km east of Lakefield, Douro Township, Ontario. BMS E25521, × 2.

6. Dorsal view of forks of hypostome showing the bevelled corrugate inner slopes of the forks. BMS E25521, × 2.

7. Hypostome, from the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. NYSM 15059, × 2.

8. Ventral view of pygidium with thoracic segments attached. Note absence of median embayment in doublure of pygidium and subparallel terraces. From the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. HMCZ 339, × 1.7.

9. Transitory pygidium with four protothoracic segements attached. Note strong segmentation. From the lower Verulam Formation (early Shermanian), Mara Limestone Quarry, Gamebridge, Mara Township, Ontario. ROM 45221, × 14.5.

10. Internal surface of incomplete dorsal shield and external surface of thoracic doublure showing panderian structures of right thoracic pleurae, oblique left lateral view. From the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. HMCZ 409, × 2.

11,12. Dorsal shield from the lower Verulam Formation (early Shermanian), roadcut on north side of Highway 401, Glen Miller, Sidney Township, Ontario. ROM 45218, × 1.6.

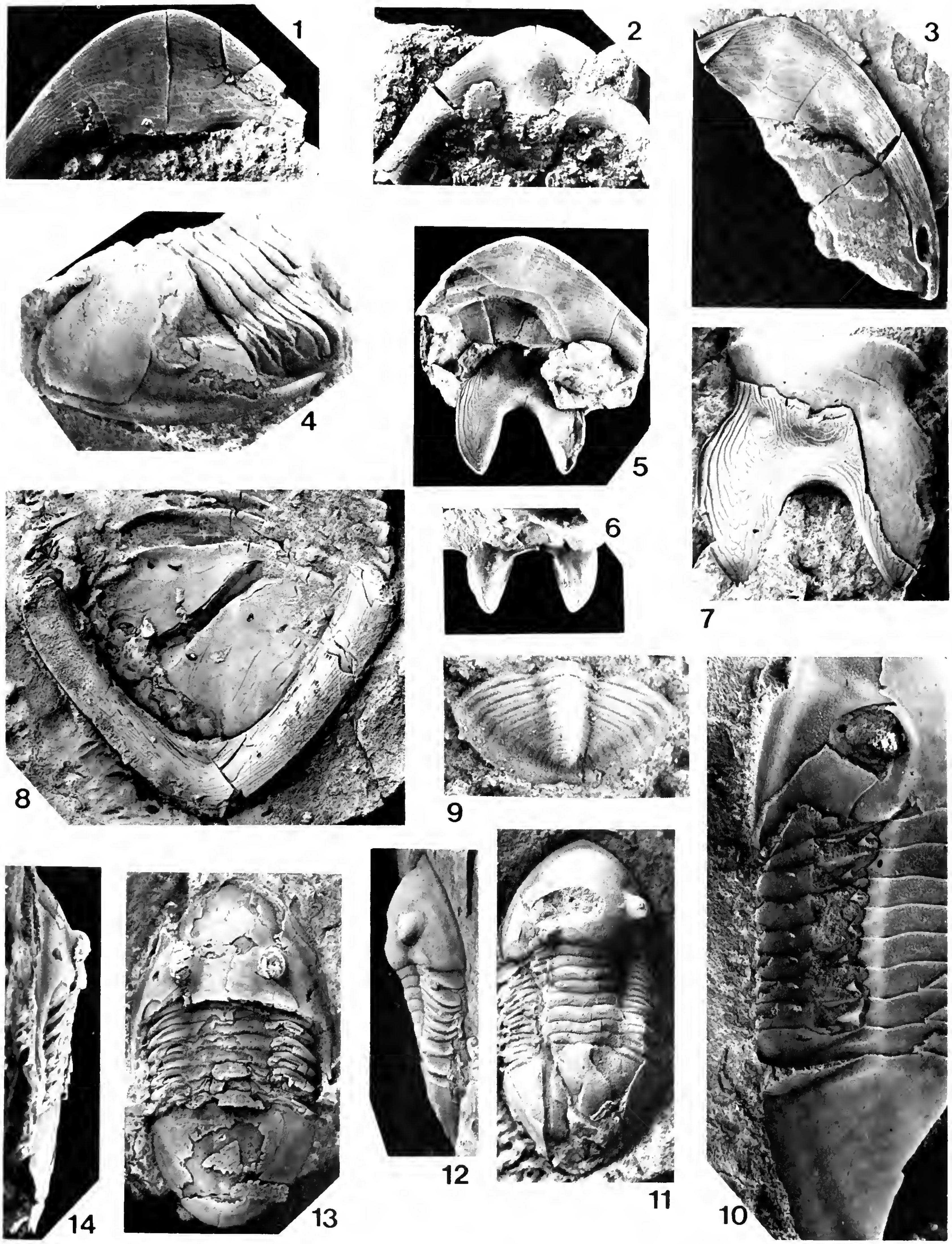
11. Dorsal view.

12. Right lateral view.

3.13,14. *Isotelus walcotti* Walcott from the Denley Formation (late Shermanian), ravine 1 km east of Sherman Fall, Trenton Falls, West Canada Creek, Herkimer County, New York. (See also Fig. 1.7.) NYSM 15058, dorsal shield, × 1.1.

13. Dorsal view.

14. Right lateral view.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