

Needmorella, a new trilobite genus of the Synphoriinae (Dalmanitidae) from the Lower–Middle Devonian of West Virginia

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Abstract.—The trilobite *Needmorella* new genus, with type species *N. simoni* new genus new species from the late Emsian to mid-Eifelian Needmore Shale of West Virginia, is a distinctive member of the subfamily Synphoriinae. It also occurs in the same formation in Pennsylvania and Virginia. It is not very similar to other Devonian representatives of the subfamily and is considered to have its origins in a morphologically less-derived ancestor because it shares certain similarities with Silurian genera, including the very short anterior cephalic border unmodified by crenulations or spines, S2 that is not largely reduced to a deep pit adaxially, the relatively low inflation of L3, and the well-defined interpleural furrows on the pygidium. Other particularly distinctive characters of the genus include the very long genal spines and the abaxially inflated and expanded posterior pleural bands on the thorax and pygidium that project slightly distally. The conventional concept of the Devonian synphoriine *Anchiopsis* Delo, 1935 appears to be incompatible with the holotype of the type species, judging from the early illustrations of the specimen, and the genus could be a synonym of *Synphoria* Clarke, 1894.

UUID: <http://zoobank.org/4a820e27-54ec-4f7b-a408-675e62b75154>

Introduction

The trilobite subfamily Synphoriinae appeared in the Silurian but attained its greatest diversity in the Early to Middle Devonian. Silurian records, ranging in age from Sheinwoodian to Gorstian, are known from regions of the United States that were situated on or close to the southern margin of the Laurentian paleocontinent, as well as from Wales and northern England (Avalonia), Sweden (Baltica), and the Prague Basin of Czechia (the Bohemian paleocontinent or Perunica) (Holloway, 1981; Storey et al., 2016). In the Devonian, the subfamily is known from the upper Lochkovian to Eifelian, with its center of radiation in the eastern United States and southeastern Canada (southern Laurussia) (Lespérance and Bourque, 1971; Lespérance, 1975; excluding *Roncellia* and *Forillonaria* of those authors, respectively, which belong to the Dalmanitinae, see Campbell, 1977). Other Devonian occurrences are in Bolivia (Holloway and Carvalho, 2010) and Colombia (Morzadec et al., 2015), which were situated on the northwestern margin of Gondwana across the Rheic Ocean from Laurussia. We here augment the Devonian record with a new synphoriine, *Needmorella simoni* n. gen. n. sp., from the Needmore Shale of West Virginia. The new genus is not very similar to other Devonian Synphoriinae, with many of the differences from them reflecting less-derived character states that are present in Silurian members of the subfamily.

Stratigraphy, fauna, and age

The Needmore Shale of the central Appalachian Basin, named by Willard (1939, p. 149), crops out in the Valley and Ridge physiographic province in central Pennsylvania, western Maryland, northeastern West Virginia, and western Virginia. It was previously referred to as the Onondaga Formation (e.g., Willard, 1936), with which it is partly correlated in the New York sequence, and in Maryland, it was also called the Onondaga Member of the Romney Formation (Kindle in Prosser et al., 1913a, p. 48, 49). The Needmore overlies the Oriskany Sandstone unconformably or disconformably and is in turn overlain conformably by the Marcellus Shale, at the base of which is the Tioga Ash Bed. In Virginia and West Virginia, the Needmore is typically 20–30 m thick (Enomoto et al., 2012, p. 3) and consists of dark- to greenish-gray shales and siltstones that are commonly calcareous and contain calcareous nodules and discrete beds of argillaceous limestone (Hunt et al., 2017, p. 62; Haynes et al., 2018, p. 14). The formation is considered to have been deposited in progressively deeper environments from ramp to basin margin, representing the beginning of foreland basin subsidence associated with the Acadian Orogeny (Haynes et al., 2018, p. 13, 43).

A diverse fossil fauna, including corals, bryozoans, brachiopods, bivalves, gastropods, cephalopods, tentaculitids, ostracods, and trilobites, was described by Kindle (1912) and Prosser et al. (1913b) from the ‘Onondaga’ (= Needmore Shale) in Pennsylvania, Maryland, Virginia, and West Virginia, with most of the named species having been previously documented from the New York sequence. Willard (1939, table 22,

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p. 156–160, pls. 16, 17, 22, 24) and Butts (1940, p. 303–305; 1941, pls. 114–117) gave extensive lists of the Needmore fauna in Pennsylvania, Virginia, and West Virginia, and also illustrated some taxa; a similar list from the formation in West Virginia was given by Woodward (1943). Cephalopods from the formation in Virginia and West Virginia were described by Miller (1938) and House (1978), as ostracods from Pennsylvania and West Virginia by Swartz and Swain (1941), rugose corals from Pennsylvania, Virginia, and West Virginia by Oliver (1989), and the trilobite *Viaphacops variabilis* (Eldredge, 1973) (= '*Phacops cristata variabilis*') from Pennsylvania by Eldredge (1973). Other authors who discussed the Needmore fauna are de Witt and Colton (1964), Inners (1979), and Newton (1979), the last recognizing the '*Phacops*,' *Planolites-Chondrites*, and *Orbiculoidea-Pacificocoelia* biofacies, corresponding to increasing depths of deposition. Burns (1991) listed a diverse fauna from the formation at four localities in West Virginia and illustrated some of the taxa in drawings. The specimens of *Needmorella simoni* n. gen. n. sp. described herein were collected from one of his localities.

Viaphacops variabilis is the only trilobite previously named based on specimens from the Needmore Shale. Other trilobites from the formation were illustrated by Kindle (1912), Butts (1941), and Burns (1991). Families represented are Proetidae, Aulacopleuridae, Brachymetopidae, Phacopidae, Dalmanitidae, Odontopleuridae, and Lichidae. Genera present, in current taxonomy and in addition to *Viaphacops* Maksimova, 1972, include *Australosutura* Campbell & Goldring in Amos et al., 1960, *Eldredgeops* Struve, 1990, *Coronura* Hall and Clarke, 1888, *Odontocephalus* Conrad, 1840, *Kettneraspis* Prantl and Přibyl, 1949, and '*Belenopyge*' Pek and Vaněk, 1991. Some of these genera have been collected by the second author at the type locality of *Needmorella simoni* n. gen. n. sp. Confirming most species assignments of previous authors is beyond the scope of the present work.

The Needmore Shale was correlated by Ver Straeten (1996, p. 20, fig. 3; 2007, fig. 18) with the Esopus, Schoharie, and Onondaga formations of New York. Conodonts from the Needmore were identified by Harris et al. (1994) as indicating an interval from the *Polygnathus costatus patulus* Biozone to the lower *Polygnathus costatus costatus* Biozone. The goniatite *Mithraxites buttsi* (Miller, 1938), documented by House (1978) as *Foordites buttsi* from high in the Needmore, was correlated by Becker and House (2000, p. 122) with the mid-Eifelian *Pinacites jugleri* Biozone. Monazite crystals from the Tioga ash bed B, at the base of the overlying Marcellus Shale, have U/Pb ages of 390.0 ± 0.5 Ma (Roden et al., 1990). All of this evidence indicates that the Needmore Shale ranges in age from late Emsian to mid-Eifelian.

Materials and methods

The specimens of *Needmorella simoni* n. gen. n. sp. were collected from the Needmore Shale in a cutting on the western side of Carpers Pike (State Route 259), ~770 m southwest of the intersection of Capon Springs Road and ~9 km northeast of Wardensville, Hampshire County, northeastern West Virginia (latitude 39.152758, longitude -78.541004). This is locality 18 of Burns (1991). The geological map of Dean et al. (1985)

places the locality at the base of the combined Needmore and Marcellus shales as depicted, just above the top of the Oriskany Sandstone. The specimens are preserved as internal and external molds in greenish gray mudstone that weathers to buff, orange-gray, or pale gray in color. The specimens have been deformed tectonically to varying degrees by shearing and crushing.

Morphological terminology follows Whittington and Kelly (1997).

Repository and institutional abbreviation.—Specimens are housed in the Department of Paleobiology, National Museum of Natural History (Smithsonian Institution), Washington, DC (USNM PAL).

Systematic paleontology

Family Dalmanitidae Vogdes, 1890

Subfamily Synphoriinae Delo, 1935

Remarks.—Silurian members of the subfamily are *Delops* Rickards, 1965 (= *Lygdozoon* Holloway, 1981), *Rickardsia* Storey, Thomas, and Owens, 2016 (= *Delops* sensu Holloway, 1981 and Šnajdr, 1982), and *Struveria* Rickards, 1965. As type species of *Delops*, Rickards (1965) designated '*Phacops obtusicaudatus* Salter, 1849 from the upper Homeric of northern England, selecting as lectotype of the species an incomplete and strongly deformed internal mold of a cephalon (Rickards, 1965, pl. 84, fig. 1; Storey et al., 2016, fig. 5A), the only other former syntype, a pygidium, having been lost. The lectotype is an unsatisfactory basis for a species, showing few distinctive features, and Rickards (1965) seems to have primarily based his concept and diagnosis of *Delops* not on *Delops obtusicaudatus* but on two other forms that he assigned to the genus, namely '*Phacops (Dalmania) nobilis* Thomas, 1900 and a newly erected subspecies '*Delops nobilis marri* Rickards, 1965. Additional and better preserved specimens of *Delops obtusicaudatus*, from the same region as the type locality and from Wales, were documented by Storey et al. (2016, fig. 5) who considered that they indicate that *Delops* is a senior subjective synonym of *Lygdozoon*, and that the species *Delops nobilis* and *Delops marri* (the latter regarded by those authors as a junior synonym of '*Dalmanites mobergi* Hede, 1915 from the Homeric of Sweden) belong to a separate genus which they named *Rickardsia*.

We exclude from Silurian representatives of the Synphoriinae the species '*Phacops weaveri* Salter, 1849, from the Telychian of Gloucestershire, England. This species was assigned to *Lygdozoon* by Curtis and Lane (1998, p. 69, pl. 8, figs. 1, 10–12) and to '*Delops sensu lato*' by Storey et al. (2016, p. 4, 5). However, its pattern of pygidial segmentation is typical of members of the Dalmanitinae, in particular the pleural furrows with abrupt anterior slopes and longer, more gentle posterior slopes, and it belongs to that subfamily (see Holloway, 1981, p. 697, 698). Also belonging to the Dalmanitinae, as indicated particularly by the spacing and form of the glabellar apodemes, is the incomplete cranidium described by Waisfeld et al. (1988, p. 316, pl. 2, fig. 14) as '*Synphoriinae gen. et sp. indet.*' from late Silurian strata of the Los Espejos Formation in the Precordillera of

Argentina. The cranium is probably conspecific with one or more of the other specimens assigned to *Dalmanites* Barrande, 1852 by those authors from the same stratigraphic section.

Of the Devonian members of the Synphoriinae, we here discuss only *Synphoria* Clarke, 1894, *Anchiopsis* Delo, 1935, and *Synphoroides* Delo, 1940, other genera being very different from *Needmorella* n. gen. *Synphoria*, with type species *Synphoria stemmata* (Clarke, 1900) from the Glenerie Formation of New York, occurs in the Pragian and possibly Emsian in eastern North America. The type species was also reported by Morzadec et al. (2015, fig. 9A–C) from the upper Emsian of Colombia, based on several pygidia, but the specimens belong to the Dalmanitinae rather than to the Synphoriinae. Authorship of *Synphoria* has generally been considered to date from Clarke (1900) (e.g., Reed, 1927, p. 343; Delo, 1935, p. 412; 1940, p. 65; Hupé, 1953, p. 235; Richter et al., 1959, p. 472; Lespérance and Bourque, 1971, p. 194; Lespérance, 1975, p. 103; Jell and Adrain, 2003, p. 450; Morzadec et al., 2015, p. 346). However, the name was first used by Clarke (1894) (to whom authorship was attributed by Reed, 1905, p. 173, and Rennie, 1930, p. 330) as a subdivision of *Dalmanites* to incorporate several taxa (*Odontocephalus*, *Corycephalus* Hall and Clarke, 1888, and *Coronura*) that at that time were also regarded as subgenera of *Dalmanites*, and that Clarke considered to be characterized by coalescence of L3 and L2 ('first and second lateral glabellar lobes,' respectively, in his terminology). This earlier usage of *Synphoria* by Clarke was considered to be nomenclatorially invalid by Delo (1940) and Richter et al. (1959) because they considered it to have been applied to a collective group of uncertain taxonomic level; for the same reason, Richter and Richter (1942, p. 175) considered that the name *Synphoria* was not valid at all. However, Clarke (1894, p. 733) clearly stated that "... for such a subgeneric division a designation is needed (e.g., *Synphoria*)." Even in the absence of that statement by Clarke (1894), the name must be regarded as having been applied to a subgenus because it was proposed for a genus-group division of the genus *Dalmanites* (ICZN, 1999, Article 10.4). No named species were assigned to *Synphoria* by Clarke (1894) but that does not affect the availability of a generic or subgeneric name established before 1931 (ICZN, 1999, Article 67.2.2).

In the case of *Anchiopsis*, there are difficulties in its interpretation and differentiation from *Synphoria*. When proposing *Anchiopsis*, with type species '*Calymene*' *anchiops* Green, 1832 from the Schoharie Formation (late Emsian) of New York, Delo (1935) did not compare it with *Synphoria*. He later stated (Delo, 1940, p. 83) that *Anchiopsis* "... marks the climax of [glabellar] lobar coalescence and elevation in the Synphoriinae," but he also noted that *Synphoria* shows similar coalescence of the lobes. He differentiated *Synphoria* from *Anchiopsis* by the less-convex cephalon, less-swollen L2 and L3, and deeper S1 and S2 of the former; however, we can see no consistent differences between the two genera in these features. *Anchiopsis anchiops* is generally considered to possess a robust occipital spine, short genal spines, and a long pygidial mucro (e.g., Hall and Clarke, 1888, pl. 9, figs. 1–5, 12, pl. 10, figs. 3–10, 12, 13; Ludvigsen, 1979, fig. 51A, B; Whiteley et al., 2002, fig. 5.2B, pl. 120), and these characters were regarded as diagnostic of the genus by Richter et al. (1959,

p. 469, 470; = '*Anchiopella*' Reed, 1907 of their usage) and Lespérance and Bourque (1971, p. 202), although *Anchiopsis armata* (Hall, 1861) has elongated genal angles lacking spines (Hall and Clarke, 1888, pl. 9, figs. 7–9; Morzadec et al., 2015, fig. 8A–D). Genal spines and a mucro can also be present in *Synphoria*; e.g., *Synphoria dolbeli* (Clarke, 1907), see Clarke (1908, pl. 8, figs. 1–7), and *Synphoria sopita* Lespérance, 1975, these species probably synonyms in our opinion. In the holotype of *Anchiopsis anchiops*, an articulated dorsal exoskeleton illustrated by Hall (1876, pl. 9, fig. 12 of Crustacea) and Hall and Clarke (1888, pl. 9, fig. 13), the occipital ring and pygidium are broken posteriorly, so it cannot be verified whether an occipital spine and mucro were originally present, as thought by Hall and Clarke (1888, explanation to pl. 9), although what is preserved of the pygidial margin suggests that it is unlikely that a mucro was present. The genal angles of the cephalon are rounded rather than spinose in the holotype. Apparently very similar to this specimen are the cephalon, lacking occipital and genal spines, and the pygidium, lacking a mucro, as illustrated by Hall (1876, pl. 9, fig. 11, pl. 10, fig. 12 of Crustacea) and Hall and Clarke (1888, pl. 9, fig. 11, pl. 10, fig. 2), both specimens also from the Schoharie Formation. These specimens are, respectively, the holotype of '*Dalmanites (Chasmops)*' *anchiops* var. *sobrinus* Hall and Clarke, 1888 and a syntype of '*Asaphus*' *laticostatus* Green, 1832, the latter being regarded by Hall (1876) and Hall and Clarke (1888) as a synonym of *Anchiopsis anchiops*. Lespérance and Bourque (1971) considered '*Dalmanites (Chasmops)*' *anchiops* var. *sobrinus* to be a possible synonym of their new subspecies *Synphoria stemmata compacta* Lespérance and Bourque, 1971, which is from the stratigraphically older (Pragian) Glenerie Formation and based on paralectotypes of the nominotypical subspecies of *Synphoria stemmata*, of which it is probably a synonym. We consider that '*Dalmanites (Chasmops)*' *anchiops* var. *sobrinus* as well as '*Asaphus*' *laticostatus* might be synonyms of *Anchiopsis anchiops*, that most specimens that have been assigned to *Anchiopsis* are not conspecific with the holotype of *Anchiopsis anchiops*, and that *Anchiopsis* might be a junior synonym of *Synphoria*. These issues can only be resolved by thorough revision of *Anchiopsis* including restudy of the type specimens of the type species as well as those of '*Dalmanites (Chasmops)*' *anchiops* var. *sobrinus* and '*Asaphus*' *laticostatus*, but that is beyond the scope of the present work.

Lespérance and Bourque (1971, pl. 27, figs. 1–3) assigned to *Anchiopsis anchiops* an exfoliated cephalon lacking a genal spine and a pygidium, from the 'upper Grande Grève Formation' (= Shiphead or Indian Cove formations in current terminology, see Lespérance, 1980; Pragian or early Emsian) of Quebec. We consider that these specimens belong to *Synphoria dolbeli*, of which the cephalon is a syntype (see Kilfoyle, 1954, p. 527) despite arguments to the contrary by Lespérance and Bourque (1971, p. 204) who referred to it incorrectly as a 'hypotype' of that species. Apparent differences between that cephalon and the other from the same formation illustrated by those authors (Lespérance and Bourque, 1971, pl. 27, figs. 6, 7) as *S. dolbeli*, in the shape of the frontal lobe and the length of the genal field in front of the eye, can be accounted for by tectonic flattening of the first specimen, and the more forwardly tilted orientation of the second (compare with the stereo-pair photographs of the second

cephalon by Lespérance, 1975, pl. 1, fig. 1). The pygidium figured as *Anchiopsis anchiops* by Lespérance and Bourque (1971) resembles in all observable characters the other pygidia figured by them as *Synphoria dolbeli* (Lespérance and Bourque, 1971, pl. 27, figs. 8, 9). The small pygidium figured as ‘*Anchiopsis* aff. *A. anchiops*’ by Lespérance and Bourque (1971, pl. 27, fig. 4) does not belong to the Synphoriinae but to the Dalmanitinae.

Synphoroides, with type species *Synphoroides biardi* (Clarke, 1907), from the upper *Rensselaeria* zone of the ‘Grande Grève Formation’ (Lespérance and Bourque, 1971, text-fig. 2), now Shiphead Formation (Pragian) of Quebec, was considered by Delo (1940, p. 78, 79) and Lespérance and Bourque (1971, p. 193) to be distinguished especially by a bifid or trifid anterior cephalic process. The lectotype cephalon of *Synphoroides biardi*, illustrated by Clarke (1908, pl. 6, fig. 8; reproduced by Delo, 1940, pl. 9, fig. 5, and Linsley, 1994, pl. 308, fig. 2), has a bifid anterior process, together with several successively smaller marginal crenulations laterally. In the other cephalon and cephalic fragments figured as *Synphoroides biardi* by Clarke (1908), the anterior process is longer and trifid. Clarke (1908, p. 264) and Delo (1940, p. 128) attributed this difference to breakage of the medial branch of the process in the lectotype but, judging from the illustrations, this appears very unlikely. The lectotype also differs from the other complete cephalon illustrated by Clarke (1908, pl. 6, fig. 12; also Delo, 1940, pl. 9, fig. 4, and Linsley, 1994, pl. 308, fig. 6) in that the glabella is narrower (tr.) across the occipital ring; the eye is larger, reaching almost to the posterior border furrow and extending closer to the lateral border furrow anterolaterally; and the genal spine is longer. Hence, if Clarke’s (1908) illustrations are accurate, it appears that the type specimens could include more than one species. Delo (1940) assigned five species to *Synphoroides* apart from the type, but two of them (‘*Dalmanites*’ *griffoni* Clarke, 1907 and ‘*Asaphus*’ *pleuroptyx* Green, 1832; the latter well illustrated by Whiteley et al., 2002, pl. 90) were rejected by Lespérance and Bourque (1971, p. 194), and we agree that these belong to the Dalmanitinae rather than to the Synphoriinae. Also belonging to the Dalmanitinae are ‘*Dalmanites*’ (*Synphoria*) ‘*esnoufi*’ Clarke, 1907 and ‘*Dalmanites*’ *multiannulatus* Ohern in Bassler et al., 1913. We tentatively retain in *Synphoroides* two other species, ‘*Dalmanites*’ *dolphii* Clarke, 1893 (see Delo, 1940, pl. 9, fig. 10), from the Port Jarvis Formation (Pragian) of New York, and *Synphoroides? vetustus* Lespérance, 1975 from the Roncelles Formation (Lochkovian?) of Quebec. However, the anterior cephalic border is poorly preserved in each and they might belong to *Synphoria*. The identification by Haas (1969, p. 651, pl. 83, figs. 5–8) of *Synphoroides biardi* from the upper Pragian of central Chihuahua, northern Mexico, was based on fragmentary cephalon and a pygidium that, judging especially from the pygidium, belong to the Dalmanitinae rather than to the Synphoriinae.

Genus *Needmorella* new genus

Type species.—*Needmorella simoni* n. gen. n. sp.

Diagnosis.—The diagnosis given for the species serves as diagnosis for the genus due to monotypy.

Etymology.—After the Needmore Shale in which the genus occurs, together with the Latin diminutive suffix *-ella*; gender feminine.

LSID.—urn:lsid:zoobank.org:act:8ECB7853-942C-4D25-8364-A11872CFEDD7.

Remarks.—*Needmorella* n. gen. is not very similar to other Devonian synphoriines. *Synphoria*, *Synphoroides*, and *Anchiopsis* (as the latter is conventionally interpreted; see preceding remarks on the subfamily) differ in that the anterior cephalic border is longer (sag., exsag.) and bears multiple crenulations or spines; the glabella is broader across L1 and does not expand as strongly forward; S2 contains an apodemal pit adaxially and is shallow or absent abaxially, so that L2 and L3 tend to coalesce; S2 and S3 extend closer to the sagittal line, the central area of the glabella being narrower; L2 and especially L3 are more inflated, at least in *Synphoria*; genal spines are much shorter or absent; the posterior pleural bands are not more inflated and expanded abaxially than the anterior bands in the thorax and pygidium; and the interpleural furrows are very weak on the pygidium. In addition, a marked subocular groove and prominent subocular ridge are present in at least *Synphoria* and *Synphoroides* (see Clarke, 1908, pl. 6, fig. 8; Lespérance, 1975, pl. 1, figs. 8, 10, pl. 2, figs. 6, 7); and on the cephalic doublure of *Synphoria*, the vincular furrow lies in front of instead of behind the prominent rounded ridge running subparallel to the cephalic margin (Clarke, 1900, pl. 2, figs. 1, 2; Lespérance and Bourque, 1971, pl. 26, fig. 4, pl. 27, fig. 6), this difference probably a result of the longer anterior border in *Synphoria*. Even more dissimilar to *Needmorella* n. gen. are *Coronura* and *Odontocephalus*, which occur together with it in the Needmore Shale.

In the very short (sag., exsag.), unmodified anterior cephalic border, S2 that is well defined abaxially, and the well-impressed pygidial interpleural furrows, *Needmorella* n. gen. resembles the Silurian synphoriines *Delops*, *Rickardsia*, and *Struveria* rather than other Devonian members of the subfamily. These similarities reflect less-derived character states. There are similarities with *Rickardsia* also in the pygidium with inflated posterior pleural bands that project slightly distally, although this feature is not as strongly developed in that genus (Rickards, 1965, pl. 84, figs. 6, 7; Storey et al., 2016, fig. 70–R). The similarities in all of these characters with Silurian members of the subfamily suggest that *Needmorella* n. gen. was not descended from the most recent common ancestor of *Synphoria* and its close allies but belongs to a morphologically more conservative lineage that did not possess the derived character states, and that persisted from the Silurian into the Devonian.

Needmorella simoni new genus new species

Figures 1–3

- 1912 *Cryphaeus* cf. *boothi* var. *calliteles* (Kayser) (sic); Kindler, p. 108, pl. 10, figs. 14, 15, pl. 11, fig. 1.
 1912 *Phaethonides gemmaeus* Hall and Clarke; Kindler, p. 111, pl. 13, fig. 12; in part, not pl. 13, fig. 11 = *Australosutura gemmaea*?
 ?1939 *Greenops boothi*, var. *calliteles*; Willard, p. 159 (list).

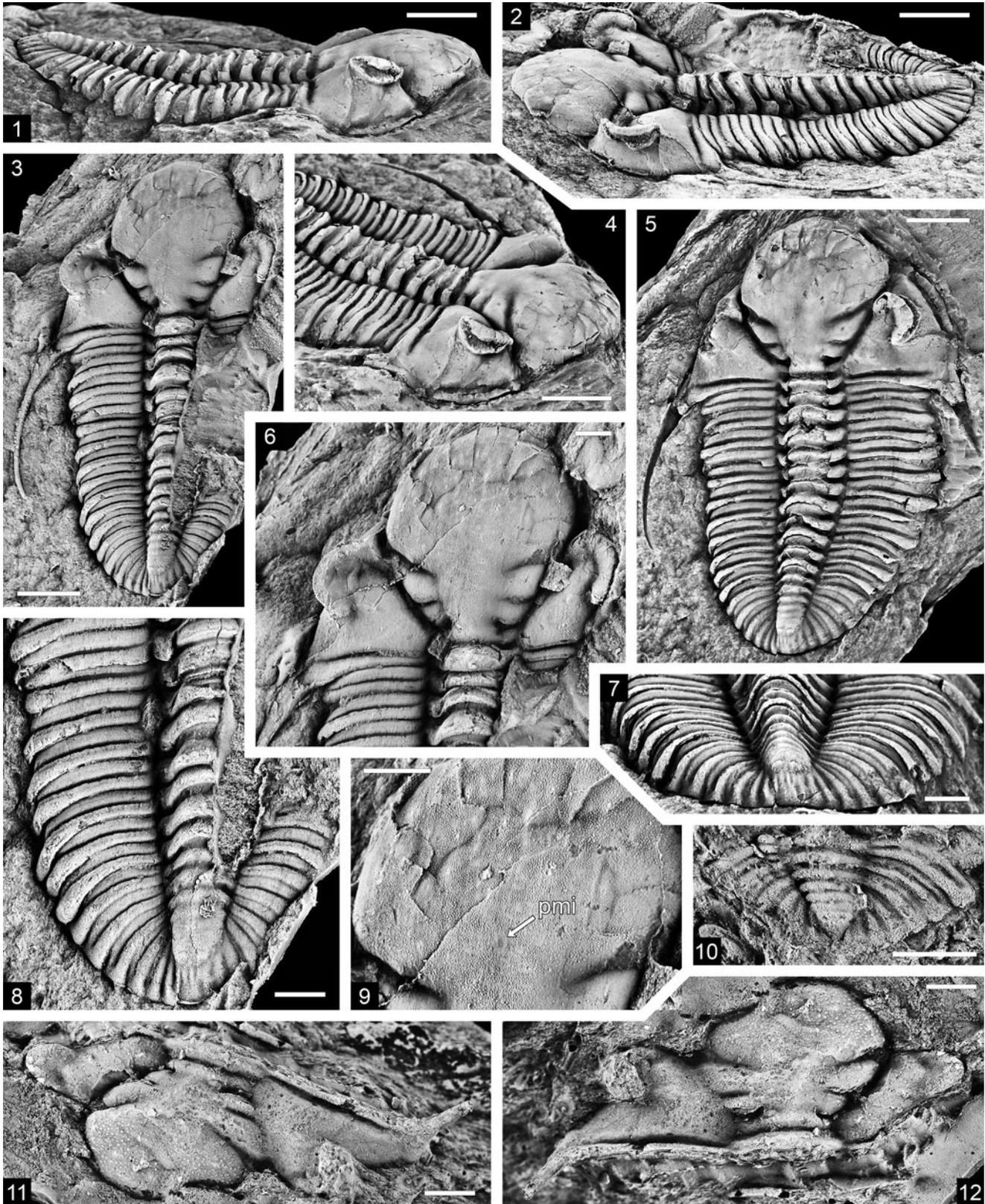


Figure 1. *Needmorella simoni* n. gen. n. sp., Needmore Shale (Emsian–Eifelian), northeastern West Virginia: (1–9) holotype, counterpart molds of dorsal exoskeleton, USNM PAL 777869A, B: (1, 4, 5, 7) internal mold, USNM PAL 777869B, lateral view, oblique view of cephalon and thorax, dorsal view, and posterodorsal view of pygidium and posterior thorax; (2, 3, 6, 8, 9) external mold, USNM PAL 777869A, latex cast, dorsolateral and dorsal views, dorsal view of cephalon and anterior thorax, dorsal view of thorax and pygidium, and detail of glabella in dorsal view showing finely granulose sculpture and posterior median impression (pmi) on frontal lobe; (10) small pygidium, USNM PAL 777876, latex cast of external mold, dorsal view; (11, 12) cranium, USNM PAL 777873, latex cast of external mold, oblique and dorsal views. Scale bars = 5 mm (1–5), 2 mm (6–12).

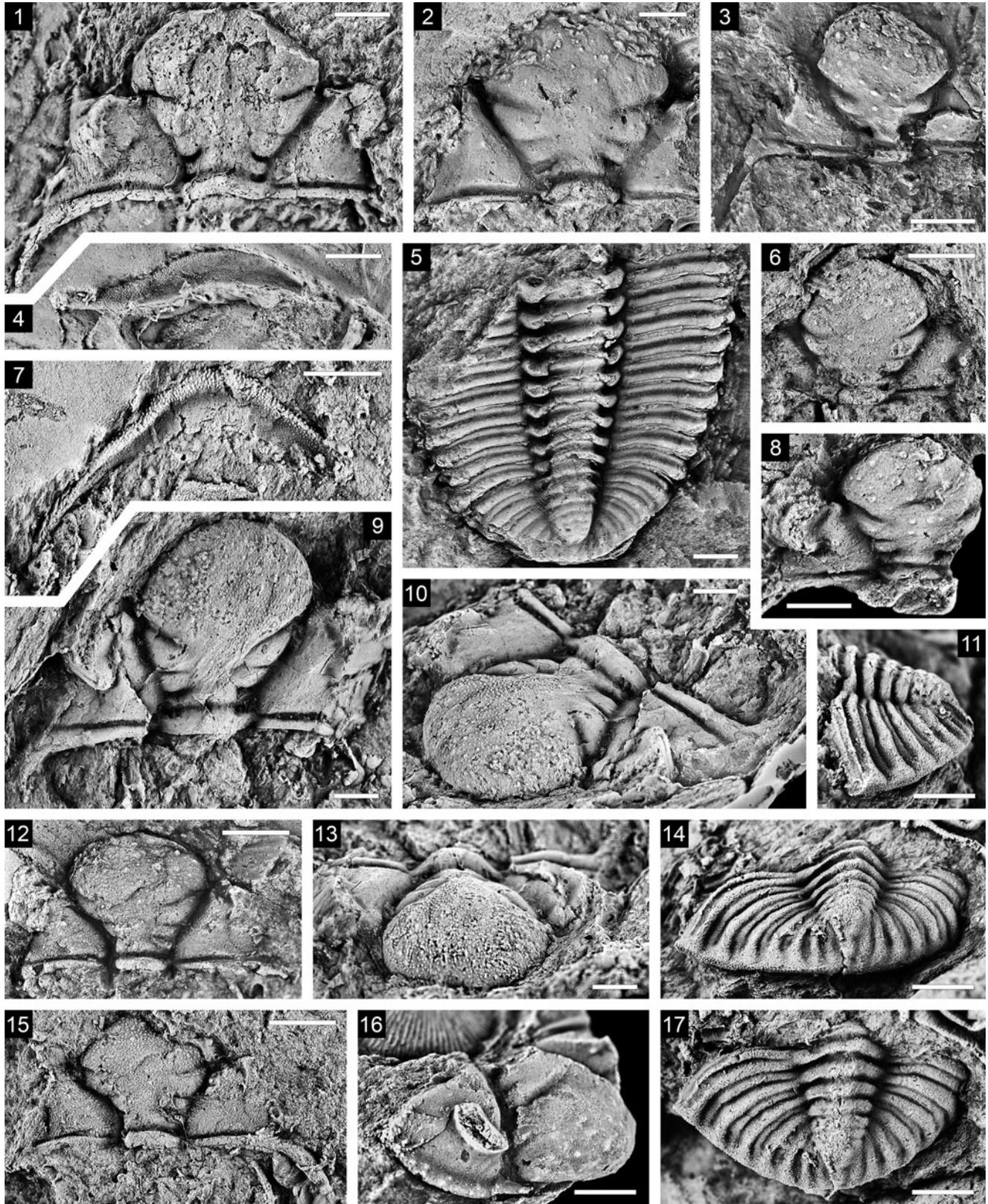


Figure 2. *Needmorella simoni* n. gen. n. sp., Needmore Shale (Emsian–Eifelian), northeastern West Virginia: (1) cranidium, USNM PAL 777877A, latex cast of external mold, dorsal view; (2) cranidium, USNM PAL 777878, internal mold, dorsal view; (3) small cranidium, USNM PAL 777883, internal mold, dorsal view; (4) cephalon, USNM PAL 777872, latex cast of external mold, detail of doublure, ventral view; (5) thoracopygon, USNM PAL 777889B, internal mold, dorsal view; (6) small cranidium, USNM PAL 777884A, latex cast of external mold, dorsal view; (7) librigenal doublure, USNM PAL 777888, latex cast of external mold, ventral view; (8) small cranidium, USNM PAL 777882B, internal mold, dorsal view; (9, 10, 13) cranidium, USNM PAL 777875, latex cast of external mold, dorsal, oblique and anterodorsal views; (11, 14, 17) pygidium, USNM PAL 777890A, latex cast of external mold, lateral, posterodorsal and dorsal views; (12, 15) counterpart molds of small cranidium, USNM PAL 777885A, B, dorsal view; (12) internal mold, USNM PAL 777885B; (15) external mold, USNM PAL 777885A, latex cast; (16) cephalon, USNM PAL 777871, internal mold, oblique view. Scale bars = 2 mm.

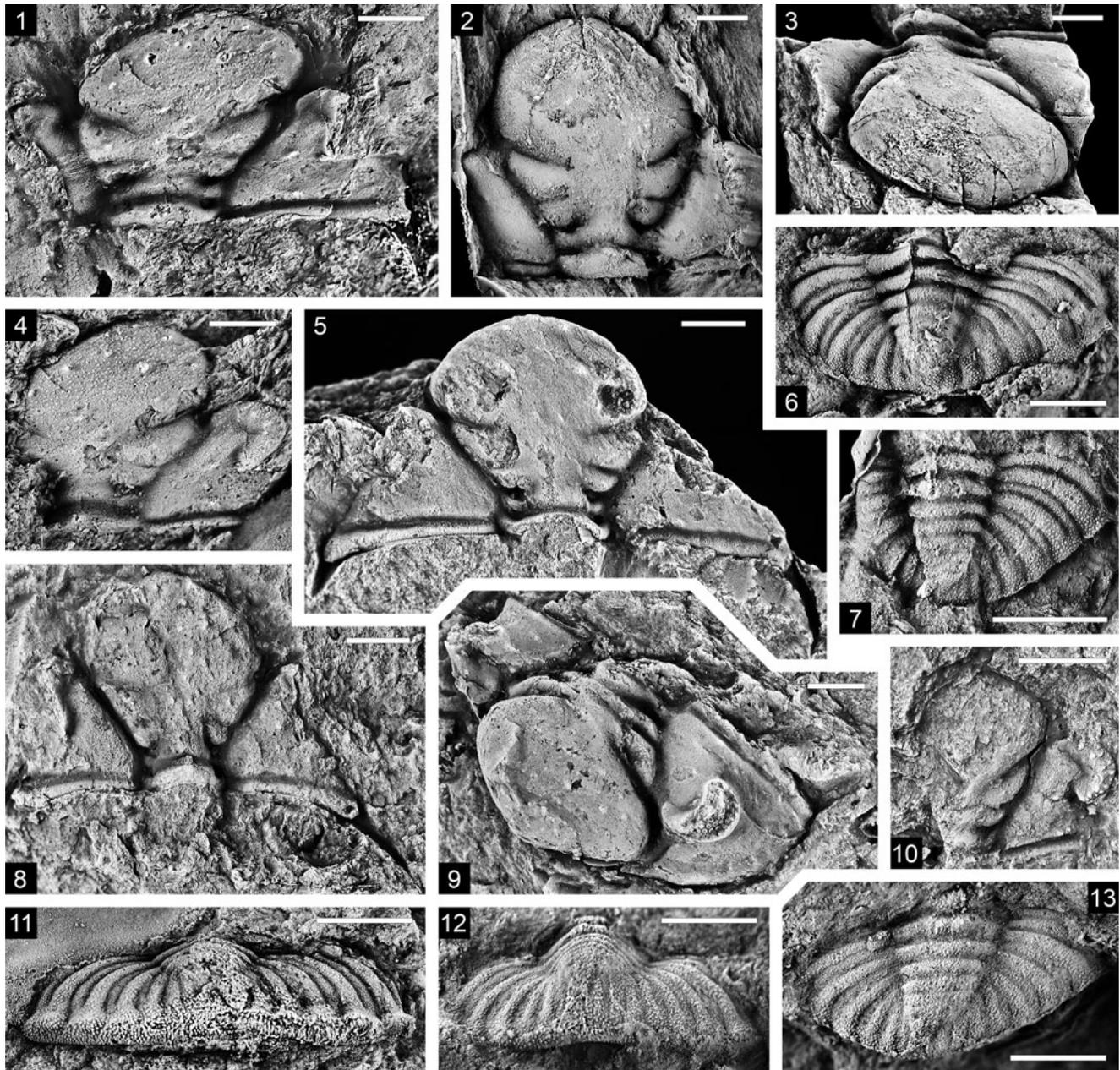


Figure 3. *Needmorella simoni* n. gen. n. sp., Needmore Shale (Emsian–Eifelian), northeastern West Virginia: (1, 4) counterpart molds of cranium, USNM PAL 777880A, B, dorsal view: (1) internal mold, USNM PAL 777880B; (4) external mold, USNM PAL 777880A, latex cast; (2, 3) counterpart molds of cranium, USNM PAL 777874A, B, dorsal view: (2) external mold, USNM PAL 777874A, latex cast; (3) internal mold, USNM PAL 777874B; (5) cranium, USNM PAL 777881, internal mold, dorsal view; (6) pygidium, USNM PAL 777891, latex cast of external mold, dorsal view; (7) small pygidium, USNM PAL 777893A, latex cast of external mold, dorsal view; (8) cranium, USNM PAL 777878B, internal mold, dorsal view; (9) cephalon, USNM PAL 777870, internal mold, oblique view; (10) small cranium, USNM PAL 777886B, internal mold, dorsal view; (11) pygidium, USNM PAL 777887A, latex cast of external mold, posterior view; (12, 13) pygidium, USNM PAL 777892, latex cast of external mold, posterior and dorsal views. Scale bars = 2 mm.

- 1941 *Dalmanites aspectans* Conrad? (sic); Butts, pl. 116, figs. 11, 12.
 ?1943 *Greenops boothi* var. *calliteles* (Green); Woodward, p. 302 (list).
 1991 *Dalmanites* sp.; Burns, fig. 15 on p. 85, fig. 4 on p. 89.

Type specimens.—Holotype, counterpart external and internal molds of articulated dorsal exoskeleton, USNM PAL 777869A, B (Fig. 1.1–1.9). Paratypes: cephalata, USNM PAL 777870–777872; cranidia, USNM PAL 777873–777875,

777877–777886; librigenal doublure, USNM PAL 777888; thoracopygon, USNM PAL 777889; pygidia, USNM PAL 777876, 777887–777894.

Diagnosis.—Anterior cephalic border very short (sag., exsag.), not modified by spines or crenulations; genal spines very long, slender, and curved; glabella expanding strongly forward in front of L1, approximately twice as wide across posterior part of frontal lobe as across L1; S2 lacking apodemal pit adaxially, meeting axial furrow abaxially; S2 and S3

extending adaxially less than half way to sagittal line, so that central area of glabella is very broad; eye of moderate size, posterior edge situated well forward opposite front of L2; cephalic doublure with vincular furrow situated behind a rounded (sag., exsag.) marginal ridge anteriorly and laterally. Pygidium nonmucronate; interpleural furrows almost as deep as pleural ones; posterior pleural bands on pygidium and posterior half of thorax increasing in convexity abaxially and expanding at expense of anterior bands, projecting slightly distally.

Occurrence.—Needmore Shale, Hampshire County, northeastern West Virginia.

Description.—Cephalon broadly parabolic in outline, its anterior margin lacking crenulations or spines (Fig. 2.4, 2.7); cephalic proportions difficult to determine due to deformation, but specimens that appear least deformed suggest that width across base of genal spines is ~170–200% length (sag.). Glabella subpentagonal in outline but well-rounded anteromedially, comprising ~25% cephalic width posteriorly (excluding genal spines), slightly narrower across L1 than across occipital ring, expanding almost uniformly from S1 to posterior part of frontal lobe except for slight outward bulge across anterior half of L3, maximum widths across L1, L2 and L3 approximately in ratio 1:1.2:1.8. Medial portion of occipital ring (approximately half total width) gently rounded (sag., exsag.) and of uniform length, lateral portion shorter and deflected forward abaxial to occipital apodemal pit; in transverse profile, occipital ring not evenly convex but strongly arched medially and gently concave on flanks (Fig. 2.13); occipital furrow transverse medially, deflected backward toward apodemal pit beyond which it is directed anterolaterally. L1 similar in appearance to occipital ring but a little shorter (sag., exsag.), less rounded (sag., exsag.) in median portion and with weak, slightly depressed lateral nodes; deep lateral portion of S1 curving forward adaxially. L2 ~150% as long (exsag.) as L1; S2 transverse or directed weakly forward adaxially, not extending as close to sagittal line as S1. L3 almost twice as long (exsag.) abaxially than adaxially where it is a little longer than L2; S3 directed obliquely backward at ~60–70° to sagittal line, its inner end more or less in line (exsag.) with that of S2. Frontal lobe comprising half sagittal glabellar length or more, subrhombic to subelliptical in outline, ~140–160% as wide as long (sag.), with small posterior median impression situated slightly behind its maximum width (Fig. 1.9). Axial furrow shallow adjacent to occipital ring and L1, well impressed from S1 to widest part of frontal lobe. Palpebral lobe convex (tr.), semicircular in lateral outline, situated approximately half its length from posterior border furrow, farther from sagittal line posteriorly than anteriorly; palpebral furrow with strongest curvature at midlength; visual surface poorly preserved due to crushing, lens arrangement indeterminate. Posterior branch of facial suture crossing gena in broad, convex-forward arc lateral to eye, meeting lateral border furrow more or less opposite ϵ (Figs. 1.5, 2.16, 3.9); anterior branch running parallel to axial furrow before curving sharply adaxially across border furrow opposite lateral extremity of frontal lobe. Fixigenal field

gently convex (exsag., tr.) adaxial to palpebral lobe and posteromedially where it is elevated above posterior border, becoming gently concave (exsag.) posterolaterally; librigenal field steeply sloping, much wider than lateral border including at front of eye (Fig. 1.1, 1.4). Posterior border approximately half as long (exsag.) proximally as lateral extremity of occipital ring, expanding slightly abaxially as far as fulcrum, thereafter expanding more strongly to approximately twice its proximal length, which it maintains for a short distance to base of genal spine (Fig. 1.6); posterior border furrow curving backward slightly beyond fulcrum, dying out distally before reaching lateral border furrow. Lateral border narrow, of uniform width, its dorsal surface gently convex; lateral border furrow shallow (Figs. 2.16, 3.9), obscured by compression fracture in holotype (Fig. 1.1, 1.4, 1.5). Genal spine initially diverging at ~30° to sagittal line, gradually tapering and curving backward and adaxially, its tip lying more or less opposite tenth thoracic segment. Cephalons and cranidia of small and moderate size with sculpture of rather sparse, coarse granules with interspersed scattered tubercles, the latter mainly on glabella and palpebral lobe; in cranidia of moderate size, tubercles mainly confined to frontal lobe but in small cranidia are also sparsely developed on L2 and L3, with apparent pairing of some tubercles here and on frontal lobe (Figs. 2.3, 2.6, 2.8, 3.4, 3.5). Sculpture on largest cephalon and cranidium consisting of very dense, fine granules, possibly superimposed on weak remnants of tubercles on frontal lobe (Figs. 1.9, 3.2).

Median part of cephalic doublure divided into rounded (sag., exsag.) outer ridge and longer (sag., exsag.), weakly convex inner portion by broad, rather shallow vincular furrow running subparallel to outer cephalic margin (Fig. 2.7); inner portion of doublure narrowing strongly laterally and vincular furrow fading; posterolaterally, only very narrow, outer portion of doublure visible in ventral view, inner portion apparently here being strongly turned upward. Hypostomal suture broadly and evenly convex forward. Sculpture of dense, coarse granules on convex outer portion of doublure, and finer, sparse granules on posterior portion and in vincular furrow (Fig. 2.4, 2.7).

Thorax composed of 11 segments, of more or less uniform width across segments 1–6 and thereafter progressively narrowing, ~70% as wide posteriorly as anteriorly. Axis subparallel-sided on segments 1–5 or 6, thereafter progressively narrowing, ~60% as wide on last segment as on first, comprising ~30% total width of first segment; axial rings similar in form to occipital ring; axial furrow bowed outward on each segment. Pleural region strongly downturned at fulcrum, situated at ~66% distance from axial furrow; pleural furrows moderately deep; anterior and posterior pleural bands weakly rounded adaxial to fulcrum, approximately equal in length (exsag.) except very close to axial furrow where posterior bands are longer as pleural furrows curve forward; abaxial to fulcrum, posterior bands increase in length and greatly in convexity.

Pygidium 160% to a little more than 200% as wide as long; maximum width level with third or fourth axial ring; posterior margin more strongly curved medially than laterally. Axis strongly convex, comprising ~25% maximum pygidial width anteriorly and 75–85% sagittal length, narrowing uniformly backward to well-defined, broadly rounded terminus; seven

axial rings plus short (sag.) terminal piece; first ring very prominent, strongly arched medially and concave on flanks like thoracic rings; subsequent rings successively less prominent and more evenly arched, second ring with weakly defined pseudoarticulating half ring; articulating furrow deep and expanded (sag., exsag.) medially, inter-ring furrows successively shorter (sag., exsag.) and shallower, weak behind third except that last appears as more distinct, paired impressions in at least some specimens (Fig. 1.5, 1.7, 1.10); articulating furrow and inter-ring furrows 1–3 or 4 containing apodemal pits laterally. Pleural region moderately convex (tr.) except close to margin where it is weakly concave; six (?), seven, or eight segments defined by inflated posterior pleural bands which, except for last few, form slight projections distally (Figs. 2.14, 3.11); shorter (exsag.) anterior pleural bands progressively reduced in development on successive segments, disappearing after fourth or fifth segment, beyond which posterior pleural bands are separated by combined pleural and interpleural furrows; holotype with weak, very narrow median postaxial ridge resembling adjacent posterior pleural bands (Fig. 1.7, 1.8); pleural and combined furrows deeper and wider (exsag.) than interpleural furrows except distally where interpleural ones deepen and expand slightly; interpleural and combined furrows extending more or less to pygidial margin, pleural furrows terminating just inside margin. Furrow behind articulating flange on anterior pleural margin extending abaxially almost to outer end of articulating facet (Fig. 2.11, 2.14, 2.17). Outer portion of doublure beneath distal projections of posterior pleural bands sloping downward and inward (Fig. 3.11). Sculpture of dense, fine granules on dorsal surface of pygidium, becoming coarser on distal ends of posterior pleural bands and outer portion of doublure.

Etymology.—After the son of the second author.

LSID.—urn:lsid:zoobank.org:act:28124EDC-79A6-41FE-900B-BC5DADA514EF.

Remarks.—Cephalae and cranidia range in length from 4.3–13.5 mm, and pygidia are ~6–11.5 mm wide. The only apparent morphological variation that can be attributed to ontogenetic change is in cephalic sculpture, rather sparse granules and scattered tubercles in small and medium-sized specimens being replaced in the largest specimens with finer, dense granules, possibly with weak remnants of tubercles on the frontal lobe. Variation in the width/length proportions of the pygidium appears to be unrelated to specimen size and is probably due largely to deformation.

We assign to *Needmorella simoni* n. gen. n. sp. the two cranidia and the dorsal exoskeleton with incomplete thorax and displaced pygidium from the ‘Onondaga’ (i.e., Needmore Shale) of West Virginia and Pennsylvania, illustrated by Kindle (1912, pl. 10, figs. 14, 15, pl. 11, fig. 1) as ‘*Cryphaeus* cf. *C. boothi* var. *calliteles*’ = *Bellacartwrightia calliteles* (Green, 1837) (see Lieberman and Kloc, 1997); Kindle incorrectly attributed authorship of this species to Kayser (1878) instead of to Green (1837). Kindle mistakenly thought that the pygidium associated with the dorsal exoskeleton might belong to another species, suggesting that he had recognized the differences from the pygidium of *Bellacartwrightia calliteles*. Coming from the

same region of Pennsylvania as the dorsal exoskeleton, and also belonging to *N. simoni* n. gen. n. sp., is the small pygidium assigned with question by Kindle (1912, pl. 13, fig. 12) to ‘*Phaethonides gemmaeus* Hall and Clarke, 1888. The other pygidium illustrated by Kindle (1912, pl. 13, fig. 11) as the latter species, from Virginia, differs markedly in proportions, pattern of segmentation, and tuberculate sculpture, and is probably correctly assigned to *Australosutura gemmaea* (Hall and Clarke, 1888). Inclusion of ‘*Greenops boothi* var. *calliteles*’ in the faunal lists of Willard (1939) and Woodward (1943) was probably based on the misidentification of this taxon by Kindle (1912). Also belonging to *N. simoni* n. gen. n. sp. are the incomplete cephalon and pygidium, from the ‘Onondaga’ in Virginia, assigned by Butts (1941, pl. 116, figs. 11, 12) to ‘*Dalmanites aspectans* Conrad?’ (= *Asaphus aspectans* Conrad, 1841), type species of *Coronura*, and probably the dorsal exoskeleton and cephalon from West Virginia illustrated as *Dalmanites* sp. in the drawings of Burns (1991, fig. 15 on p. 85, fig. 4 on p. 89).

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Declaration of competing interests

The authors declare none.

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