

One name to rule them all: *Belinurus trilobitoides* (Buckland, 1837) is senior synonym to fourteen named species

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One of the oldest fossil horseshoe crabs figured in the literature is *Entomolithus lunatus* Martin, 1809, a Carboniferous species included in his *Petrificata Derbiensia*. While the species has generally been included within the genus *Belinurus* Bronn, 1839, it was recently used as the type species of the new genus *Parabelinurus* Lamsdell, 2020. However, recent investigation as to the appropriate authority for *Belinurus* (see Lamsdell and Clapham, 2021) revealed that all the names in *Petrificata Derbiensia* were suppressed in Opinion 231 of the International Commission on Zoological Nomenclature (1954) for being consistently nonbinomial under Article 11.4 of the International Code of Zoological Nomenclature (ICZN) (International Commission on Zoological Nomenclature, 1999). Despite the validation of several species names for anthozoans, brachiopods, and cephalopods described in *Petrificata Derbiensia* in subsequent rulings (International Commission on Zoological Nomenclature, 1956a, b), *Belinurus lunatus* has not been the subject of any subsequent Commission ruling or opinion, and so its use in *Petrificata Derbiensia* remains suppressed. The *Belinurus lunatus* species name was used in several subsequent publications during the 1800s, none of which made the name available under ICZN article 11.5; Parkinson (1811) is also suppressed for being nonbinomial, while Woodward (1830), Buckland (1837), Bronn (1839), and Baily (1859) refer to the species only as a synonym of *Belinurus trilobitoides* (Buckland, 1837) through citation to the suppressed *Petrificata Derbiensia*. The first author to make *Belinurus lunatus* an available name was Baldwin (1905), who used the name in reference to a new figured specimen from Sparth Bottoms, Rochdale, UK, but again as an explicit junior synonym of *Belinurus trilobitoides* (Buckland, 1837). Therefore, it was not until Eller (1938) treated *B. lunatus* as a distinct species from *B. trilobitoides* that *B. lunatus* became an available name as per ICZN Article 11.6.1 under the authorship of Baldwin (1905) following ICZN Article 50.7.

When Eller (1938) made *B. lunatus* available, he did so seemingly unwittingly, with no reference to distinguishing characteristics. *Belinurus lunatus* is furthermore noticeably absent from otherwise comprehensive species lists (e.g., Raymond, 1944; Morris, 1980). Prantl and Přibyl (1955) correctly listed *B. lunatus* as a synonym of *B. bellulus* (itself a junior synonym of *B. trilobitoides*); Filipiak and Krawczyński (1996) deferred to (but did not reiterate) Prantl and Přibyl's (1955) synonymy, but incorrectly retained *B. lunatus* under Martin (1809) as the senior species. *Belinurus lunatus*, therefore, is and always has been a junior synonym of *B. trilobitoides*.

Lamsdell (2020) and Bicknell and Pates (2020) both erroneously included *B. lunatus* as a valid species, referring particularly to Filipiak and Krawczyński's (1996) treatment of the species. In coding the species for phylogenetic analysis, Lamsdell (2016, 2020) referred extensively to Filipiak and Krawczyński's (1996) material, which incidentally comprises predominantly large individuals. On the basis of the resulting tree topology, Lamsdell proposed the new genus *Parabelinurus*, with *P. lunatus* (Martin) as the type species. As *P. lunatus* and *B. trilobitoides* are synonyms, *Parabelinurus* Lamsdell, 2020 and *Belinurus* Bronn, 1839 are objective synonyms. Thirteen other *Belinurus* species have also been proposed as synonyms with *B. trilobitoides*, with their constituent specimens representing taphonomic or ontogenetic variants (Fisher, 1975; Anderson, 1996; Haug and Haug, 2020), including the type species of further genera considered valid by Lamsdell (2020), *Koenigiella* Raymond, 1944 and *Macrobelinurus* Lamsdell, 2020. To clarify this issue for future researchers, a full taxonomic history of *Belinurus trilobitoides* (Buckland, 1837), including all synonymies, is presented here.

Systematic paleontology

Belinurus Bronn, 1839

(= *Bellinurus* Pictet, 1846; = *Steropis* Baily, 1859; = *Koenigiella* Raymond, 1944; = *Macrobelinurus* Lamsdell, 2020; = *Parabelinurus* Lamsdell, 2020)

Type species.—*Limulus trilobitoides* (Buckland, 1837), by subsequent designation (= *Belinurus bellulus* König, c.1851/Pictet, 1854; = *Steropis arcuatus* Baily, 1859; = *Belinurus reginae* Baily, 1863; = *Belinurus koenigianus* Woodward, 1872; = *Bellinurus grandaevus* Jones and Woodward, 1899; = *Parabelinurus lunatus* (Baldwin, 1905); = *Bellinurus baldwini* Woodward, 1907; = *Bellinurus longicaudatus* Woodward, 1907; = *Bellinurus trechmanni* Woodward, 1918; = *Belinurus concinnus* Dix and Pringle, 1929; = *Belinurus carwayensis* Dix and Pringle, 1929; = *Belinurus truemani* Dix and Pringle, 1929; = *Belinurus pustulosus* Dix and Pringle, 1929; = *Belinurus morgani* Dix and Pringle, 1930).

Other species.—? *Belinurus iswariensis* (Chernyshev, 1928); ? *Belinurus kitorcanensis* Baily, 1869; *Belinurus lacoei* (Packard, 1885); ? *Belinurus metschensis* (Chernyshev, 1928); *Belinurus silesiacus* (Roemer, 1883); ? *Belinurus stepanovi* (Chernyshev, 1928); *Belinurus sustai* (Prantl and Přibyl, 1955).

Diagnosis.—Belinurid with ophthalmic spines positioned at posterior of ophthalmic ridges; axis of first thoracetron tergite medially inflated; thoracetron ovoid to semicircular in outline; thoracetron fixed tergopleural spines elongate, needle-like; conical opisthosomal boss present (after Lamsdell, 2020).

Remarks.—The correct authorship and spelling of *Belinurus* was recently clarified by Lamsdell and Clapham (2021), who demonstrated that *Belinurus* Bronn, 1839 was the correct spelling and attribution as opposed to *Bellinurus* Pictet, 1846.

?*Belinurus kiltorcanensis* is known only from an isolated carapace that exhibits ophthalmic ridges similar to those in *Belinuroopsis* and may not be a *Belinurus*. The *Belinurus* species described by Chernyshev (1928) need restudy to ascertain their placement within the genus.

Belinurus trilobitoides (Buckland, 1837)

Figure 1

- 1809 'Entomolithus Monoculites? (lunatus)'; Martin, p. 191, pl. 45, fig. 4.
- 1811 'Monoculites lunatus'; Parkinson, p. 275, pl. 18, fig. 18.
- 1830 'Entomolithus Derbyensis lunatus'; Woodward, p. 8.
- 1837 *Limulus trilobitoides* Buckland, p. 77, pl. 46", fig. 3.
- 1839 'Belinurus monoculites'; Bronn, p. 489.
- 1839 *Belinurus trilobitoides*; Bronn, p. 489.
- 1840 *Limulus trilobitoides*; Prestwich, p. 491, pl. 41, fig. 8.
- 1843 *Limulus trilobitoides*; Morris, p. 75.
- 1850 *Limulus trilobitoides*; Mantell, p. 156, pl. 68, fig. 15.
- c.1851 *Belinurus bellulus* König, pl. 28, fig. 230.
- 1854 *Bellinurus bellulus*; Pictet, p. 538, pl. 46, fig. 23.
- 1859 *Steropsis arcuatus* Baily, p. 90.
- 1859 *Steropsis trilobitoides*; Baily, p. 91.
- 1859 'Steropsis monoculus'; Baily, p. 91.
- 1859 *Steropsis bellulus*; Baily, p. 91.
- 1863 *Belinurus reginae* Baily, p. 110, pl. 5, fig. 1A–D.
- 1863 *Belinurus arcuatus*; Baily, p. 111, pl. 5, fig. 2A–C.
- 1867 *Belinurus trilobitoides*; Woodward, p. 32.
- 1867 *Belinurus reginae*; Woodward, p. 32, pl. 1, fig. 1.
- 1867 *Belinurus arcuatus*; Woodward, p. 32.
- 1872 *Limulus trilobitoides*; Woodward, p. 439.
- 1872 *Bellinurus bellulus*; Woodward, p. 439.
- 1872 *Bellinurus reginae*; Woodward, p. 439.
- 1872 *Bellinurus arcuatus*; Woodward, p. 439.
- 1872 *Bellinurus koenigianus* Woodward, p. 439, pl. 10, fig. 8.
- 1878 *Bellinurus bellulus*; Woodward, p. 239, pl. 31, fig. 3a–c.
- 1878 *Bellinurus reginae*; Woodward, p. 240, pl. 31, fig. 1a–d.
- 1878 *Bellinurus arcuatus*; Woodward, p. 241, pl. 31, fig. 2a, b.
- 1878 *Bellinurus koenigianus*; Woodward, p. 243, pl. 31, figs. 3c, 4.
- 1899 *Bellinurus grandaevus* Jones and Woodward, p. 388, pl. 15, figs. 2, 3.
- 1903 *Belinurus bellulus*; Baldwin, p. 198.
- 1905 *Belinurus lunatus* Baldwin, p. 136, fig. 2.
- 1907 *Belinurus lunatus*; Parker, p. 44.
- 1907 *Bellinurus baldwini* Woodward, p. 540, fig. 1.
- 1907 *Bellinurus longicaudatus* Woodward, p. 451, fig. 2.
- 1908 *Belinurus baldwini*; Parker, p. 71.
- 1908 *Belinurus longicaudatus*; Parker, p. 72.
- 1909 *Belinurus baldwini*; Parker, p. 6.
- 1909 *Belinurus longicaudatus*; Parker, p. 6.
- 1911 *Belinurus reginae*; Pruvost, p. 299, pl. 7, fig. 4, 4a.
- 1918 *Bellinurus trechmanni* Woodward, p. 462, fig. 5.
- 1929 *Belinurus concinnus* Dix and Pringle, p. 92, fig. 1.
- 1929 *Belinurus carwayensis* Dix and Pringle, p. 93, fig. 2.
- 1929 *Belinurus truemani* Dix and Pringle, p. 94, fig. 3.
- 1929 *Belinurus pustulosus* Dix and Pringle, p. 95, fig. 4.
- 1929 *Belinurus bellulus*; Dix and Pringle, p. 97, fig. 5.
- 1929 *Belinurus arcuatus*; Dix and Pringle, p. 98, fig. 6.
- 1929 *Belinurus* cf. *B. arcuatus*; Dix and Pringle, p. 99, fig. 7.
- 1929 *Belinurus* cf. *B. koenigianus*; Dix and Pringle, p. 100, fig. 8.
- 1930 *Belinurus reginae*; Pruvost, p. 197, pl. 12, fig. 5.
- 1930 *Belinurus lunatus*; Pruvost, p. 198, pl. 12, figs. 7, 8.
- 1930 *Belinurus koenigi*; Pruvost, p. 199, pl. 12, fig. 6.
- 1930 *Belinurus morgani* Dix and Pringle, p. 137, fig. 1.
- 1930 *Belinurus* cf. *B. truemani*; Dix and Pringle, p. 138, fig. 2.
- 1930 *Belinurus bellulus*; Dix and Pringle, p. 139, fig. 3.
- 1930 *Belinurus koenigianus*; Dix and Pringle, p. 141.
- 1930 *Belinurus reginae*; Dix and Pringle, p. 141.
- 1938 *Belinurus bellulus*; Eller, p. 132, p. 10, figs. 3–10.
- 1938 *Belinurus koenigianus*; Eller, p. 132, pl. 9, fig. 3, pl. 11., figs. 1, 2, 8.
- 1938 *Belinurus grandaevus*; Eller, p. 132, pl. 12, figs. 7, 8.
- 1938 *Belinurus pustulosus*; Eller, p. 133, pl. 12, fig. 9.
- 1938 *Belinurus reginae*; Eller, p. 133, pl. 10, figs. 1, 2.
- 1938 *Belinurus arcuatus*; Eller, p. 133, pl. 11, figs. 3–6.
- 1938 *Belinurus lunatus*; Eller, p. 133, pl. 14, fig. 3.
- 1938 *Belinurus baldwini*; Eller, p. 133, pl. 14, fig. 1.
- 1938 *Belinurus longicaudatus*; Eller, p. 133, pl. 14, fig. 2.
- 1938 *Belinurus truemani*; Eller, p. 134, pl. 11, fig. 7.
- 1938 *Belinurus concinnus*; Eller, p. 134, pl. 12, fig. 5.
- 1938 *Belinurus carwayensis*; Eller, p. 134, pl. 12, fig. 6.
- 1938 *Belinurus morgani*; Eller, p. 134, pl. 12, fig. 2.
- 1938 *Belinurus trechmanni*; Eller, pl. 12, fig. 1.
- 1944 *Belinurus concinnus*; Raymond, p. 480.
- 1944 *Belinurus grandaevus*; Raymond, p. 480.
- 1944 *Belinurus bellulus*; Raymond, p. 480.
- 1944 *Belinurus truemani*; Raymond, p. 480.
- 1944 *Belinurus morgani*; Raymond, p. 480.
- 1944 *Belinurus pustulosus*; Raymond, p. 480.
- 1944 *Koenigiella reginae*; Raymond, p. 480.
- 1944 *Koenigiella arcuata*; Raymond, p. 480.
- 1944 *Koenigiella koenigiana*; Raymond, p. 480.
- 1951 *Belinurus reginae*; van der Heide, pl. 7, figs. 2, 5.
- 1952 *Belinurus reginae*; Størmer, p. 635.
- 1952 *Belinurus bellulus*; Størmer, p. 635.
- 1955 *Belinurus regina*; Størmer, p. 20, fig. 13.1a.
- 1955 *Belinurus arcuatus*; Størmer, p. 20, fig. 13.1b.
- 1955 *Belinurus baldwini*; Størmer, p. 20, fig. 13.1c.
- 1955 *Belinurus bellulus*; Prantl and Přibyl, p. 385, pl. 1, figs. 1, 2.
- 1957 *Belinurus reginae*; Copeland, p. 48, pl. 16, figs. 2, 9, 10.
- 1957 *Belinurus grandaevus*; Copeland, p. 48, pl. 16, figs. 1, 3–8.
- 1975 *Belinurus koenigianus*; Bergström, p. 294, pl. 1, fig. 5.
- 1980 *Belinurus bellulus*; Morris, p. 31.
- 1980 *Bellinurus baldwini*; Morris, p. 31.
- 1980 *Bellinurus koenigianus*; Morris, p. 31.
- 1980 *Bellinurus longicaudatus*; Morris, p. 31.

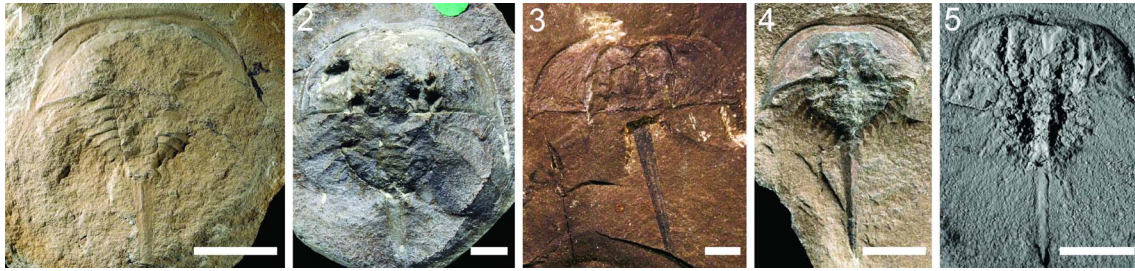


Figure 1. Specimens of *Belinurus trilobitoides* previously considered to represent distinct species and genera. (1) MM LL.111267a, assigned to *Belinurus trilobitoides*. (2) NHMUK PI. I. 2754, previously assigned to *Belinurus lunatus*. (3) GSC 12803, previously assigned to *Belinurus reginae*. (4) NHMUK PI. In. 18572, holotype of *Belinurus baldwini*. (5) AM F29886, previously assigned to *Belinurus arcuatus*. Scale bars = 5 mm. Institutional abbreviations: AM = Australian Museum, Sydney, Australia; GSC = Geological Survey of Canada, Ottawa, Canada; MMUP = Manchester Museum, Manchester, UK; NHMUK = Natural History Museum, London, UK. (1, 2, 4, 5) Images reproduced from Bicknell and Pates (2020) under a CC BY 4.0 license.

- 1980 *Bellinurus trilobitoides*; Morris, p. 31.
 1981 *Belinurus koenigianus*; Fisher, p. 51, fig. 3A.
 1984 *Belinurus reginae*; Fisher, p. 199.
 1984 *Belinurus bellulus*; Fisher, p. 199.
 1984 *Belinurus koenigianus*; Fisher, p. 199.
 1987 *Bellinurus koenigianus*; Selden and Siveter, p. 384.
 1994 *Bellinurus grandaevus*; Schultka, p. 347.
 1994 *Bellinurus arcutus*; Schultka, p. 347.
 1994 *Bellinurus reginae*; Schultka, p. 347.
 1994 *Bellinurus lunatus*; Schultka, p. 347.
 1994 *Bellinurus concinnus*; Schultka, p. 347.
 1994 *Bellinurus longicaudatus*; Schultka, p. 347.
 1994 *Bellinurus koenigianus*; Schultka, p. 347.
 1994 *Bellinurus baldwini*; Schultka, p. 347.
 1994 *Bellinurus bellulus*; Schultka, p. 347.
 1994 *Bellinurus carwayensis*; Schultka, p. 347.
 1994 *Bellinurus morgani*; Schultka, p. 347.
 1994 *Bellinurus truemani*; Schultka, p. 347.
 1994 *Bellinurus trechmannii*; Schultka, p. 347.
 1996 *Bellinurus lunatus*; Filipiak and Krawczyński, p. 420, fig. 4C–H.
 1997 *Bellinurus truemani*; Anderson and Selden, p. 20.
 1997 *Bellinurus morgani*; Anderson and Selden, p. 20.
 1997 *Bellinurus koenigianus*; Anderson and Selden, p. 20.
 1997 *Bellinurus trilobitoides*; Anderson and Selden, p. 20, fig. 1.
 1997 *Bellinurus arcuatus*; Anderson and Selden, p. 20.
 1997 *Bellinurus trilobitoides*; Anderson et al., p. 203, fig. 4a, b.
 2016 *Bellinurus arcuatus*; Lamsdell, p. 182.
 2016 *Bellinurus bellulus*; Lamsdell, p. 182.
 2016 *Bellinurus lunatus*; Lamsdell, p. 182.
 2016 *Bellinurus reginae*; Lamsdell, p. 182.
 2016 *Bellinurus trilobitoides*; Lamsdell, p. 182.
 2016 *Bellinurus truemani*; Lamsdell, p. 182.
 2020 *Bellinurus arcuatus*; Bicknell and Pates, p. 18, fig. 13C.
 2020 *Bellinurus baldwini*; Bicknell and Pates, p. 18, fig. 13E.
 2020 *Bellinurus bellulus*; Bicknell and Pates, p. 18, fig. 13D.
 2020 *Bellinurus carwayensis*; Bicknell and Pates, p. 18, fig. 13F.
 2020 *Bellinurus concinnus*; Bicknell and Pates, p. 18, fig. 14B.
 2020 *Bellinurus koenigianus*; Bicknell and Pates, p. 18, fig. 14E.
 2020 *Bellinurus longicaudatus*; Bicknell and Pates, p. 18, fig. 15C.
 2020 *Bellinurus lunatus*; Bicknell and Pates, p. 18, fig. 15A, B.
 2020 *Bellinurus pustulosus*; Bicknell and Pates, p. 18, fig. 16D.
 2020 *Bellinurus reginae*; Bicknell and Pates, p. 19, fig. 16C, E.
 2020 *Bellinurus trechmannii*; Bicknell and Pates, p. 19, fig. 17B.
 2020 *Bellinurus trilobitoides*; Bicknell and Pates, p. 19, fig. 17D.
 2020 *Bellinurus truemani*; Bicknell and Pates, p. 19, fig. 17C.
 2020 '*Belinurus* sp.'; Haug and Haug, figs. 1I–VI, 3, 4, 5, 8a–f, 10a–c.
 2020 *Belinurus bellulus*; Lamsdell, p. 13.
 2020 *Belinurus carwayensis*; Lamsdell, p. 13, fig. 1G.
 2020 *Belinurus concinnus*; Lamsdell, p. 13.
 2020 *Belinurus grandaevus*; Lamsdell, p. 13.
 2020 *Belinurus morgani*; Lamsdell, p. 13, fig. 1J.
 2020 *Belinurus pustulosus*; Lamsdell, p. 13.
 2020 *Belinurus trechmannii*; Lamsdell, p. 14.
 2020 *Belinurus trilobitoides*; Lamsdell, p. 14.
 2020 *Koenigiella reginae*; Lamsdell, p. 14.
 2020 *Koenigiella baldwini*; Lamsdell, p. 15.
 2020 *Koenigiella koenigianus*; Lamsdell, p. 15.
 2020 *Koenigiella longicaudatus*; Lamsdell, p. 15.
 2020 *Koenigiella truemani*; Lamsdell, p. 15.
 2020 *Macrobellinurus arcuatus*; Lamsdell, p. 15.
 2020 *Parabellinurus lunatus*; Lamsdell, p. 15.
- Lectotype*.—Complete individual preserving dorsal exoskeleton, comprising prosomal carapace, thoracetrone, and telson (BNMH 34889) from the Carboniferous clay ironstone of the Coalbrookdale Coal Measures, Telford, Shropshire (Buckland, 1837, pl. 46", fig. 3).
- Remarks*.—Fifteen of the 22 species historically included within *Belinurus* have been considered synonyms after critical evaluation by a number of researchers (Fisher, 1975; Anderson, 1996), with many regularly co-occurring (e.g., *B. reginae* and *B. grandaevus* in Nova Scotia, Canada (Copeland, 1957); *B. arcuatus* and *B. reginae* in Leinster, Ireland (Baily, 1863); *B. trilobitoides*, *B. lunatus*, *B. longicaudatus*, and *B. baldwini* in Rochdale, UK (Eller, 1938); *B. morgani*, *B. trilobitoides*, and *B. reginae* in Neath, Wales (Dix and Pringle, 1930)). Haug and Haug (2020), in reconstructing an ontogenetic series of *Belinurus* specimens based on material held in the Natural History Museum, London (BMNH), did not refer to the previous species assignments of individual specimens but included numerous specimens referred to *B. trilobitoides* (BMNH 18357, 18565, 18571, 36188, 13897, 13898, 13958, In41494, 46421) along with the holotypes of *B. baldwini* (BMNH

In 18572), *B. koenigianus* (BMNH In59227), and *B. trechmanni* (BMNH In18487) as different ontogenetic stages of the same species.

Most of the 14 junior synonyms of *B. trilobitoides* were diagnosed on the basis of dubious morphological criteria that are now known to be the result of taphonomic or ontogenetic processes, a conclusion supported by recent increases in our understanding of horseshoe crab decay (Babcock and Chang, 1997) and development (Haug et al., 2012; Haug and Rötzer, 2018; Tashman et al., 2019; Haug and Haug, 2020; Lamsdell, 2021). *Belinurus arcuatus* (the type species of *Macrobelinurus* Lamsdell, 2020), known from an isolated carapace, was diagnosed on the basis of the presence of a “facial suture” that is actually a crease in a taphonomically deformed specimen that otherwise exhibits no clear differences from specimens of *B. trilobitoides*. *Belinurus reginae* (type species of *Koenigiella* Raymond, 1944) was diagnosed solely on the occurrence of long thoracetrone epimera, a trait known to vary throughout ontogeny. *Belinurus koenigianus* was diagnosed on the basis of the lack of carapace spines (which are actually broken away from the specimen rather than absent) and the proportions of the thoracetrone, which is laterally compressed. No diagnosis was presented for *B. grandaevus*, which appears to have been named solely due to its geographic occurrence, and the available material shows no obvious differences from *B. trilobitoides*. Baldwin (1905) explicitly named *B. lunatus* as a junior synonym of *B. trilobitoides* and as such provided no diagnostic differences. *Belinurus baldwini* was defined as a species on the basis of carapace dimensions; however, the type specimen is taphonomically distorted and no other characters separate it from *B. trilobitoides*. *Belinurus longicaudatus* was diagnosed solely on its possession of a long telson although telson length is known to vary between individuals and through ontogeny. *Belinurus trechmanni* is known from a small specimen and diagnosed on the basis of genal spine length and thoracetrone shape, both of which change through ontogeny. Finally, Dix and Pringle (1929, 1930) named *B. concinnus*, *B. carwayensis*, *B. truemanni*, and *B. morgani* on the basis of their possession of different numbers of free segments in the thoracetrone, an interpretation of segment articulation now recognized as erroneous (Anderson and Selden, 1997). *Belinurus truemanni* was further diagnosed by the possession of curved genal spines (the form of which is due to compression), *B. concinnus* by a long headshield (when the specimen is tectonically distorted), and *B. morgani* by granulation on the prosoma (which is also known from *B. trilobitoides*). The final synonymous species, *B. pustulosus*, was diagnosed on the basis of a pustulose cuticular ornament, which again does not serve to distinguish the specimens from *B. trilobitoides*. With none of these species having valid diagnostic traits to separate them from *B. trilobitoides*, the weight of evidence suggests that all are considered synonyms, in keeping with the conclusions of Fisher (1975), Anderson (1996), and Haug and Haug (2020).

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