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Paradoxides brachyrhachis Linnarsson, 1883 versus *Paradoxides mediterraneus* Pompeckj, 1901: a problematic determination

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Abstract: A revision of paradoxidid trilobites reveals that previous identifications of specimens from Sardinia and Spain as the Nordic trilobite species *Paradoxides brachyrhachis* Linnarsson, 1883, are mistaken. The southern species, occurring also in France, is here referred to *Eccaparadoxides mediterraneus* (Pompeckj, 1901). Main differences are seen in the preocular field, pleural furrow and pygidium. The species *P. brachyrhachis* is referred with question to the genus *Mawddachites* Fletcher 2007.

Keywords: Trilobites, *Eccaparadoxides mediterraneus*, *Mawddachites*? *brachyrhachis*, middle Cambrian, Scandinavia, Sardinia, Spain, Mediterranean subprovince.

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Introduction

The middle Cambrian (Cambrian provisional Series 3) agnostoid and trilobite faunas of the Mediterranean and Baltic provinces are diverse, but have relatively few taxa in common. Álvaro et al. (2003, p. 22) tabulated more than fifty genera from the Mediterranean area (including Morocco) and over forty from Baltica, but fewer than half of them are known to occur in both regions. Hundreds of species have been described from the traditional middle Cambrian of the Mediterranean and Baltic provinces, but there are very few common to both: a few agnostoids such as *Condylopyge rex* (Barrande, 1846), *Peronopsis fallax* (Linnarsson, 1869) sensu lato, and *Peronopsis acadica* Hartt (*in* Dawson, 1868); and among the trilobites proper *Acadoparadoxides mureroensis* (Sdzuy, 1958) (in Poland), *Parasolenopleura aculeata* (Angelin, 1851), and possibly also *Paradoxides davidis* Salter, 1863.

Among the host of corynexochid and solenopleuroid species, there is scarcely a species in common. It is interesting, therefore, that '*Paradoxides brachyrhachis* Linnarsson, 1883', originally described from Andrarum in Scania (Skåne), southern Sweden, has been recorded in abundance from localities in Spain (e.g. Sdzuy 1961, p. 608; Liñán & Gozalo 1986, p. 56) and in the Montagne Noire, southern France (Courtessole 1973, p. 126). This species has been used both in the development of a paradoxidid zonation in the Spanish Cesaraugustan successions and in providing a good example of the inferred sexual dimorphism in paradoxidid trilobites (Gozalo et al. 2003).

A review of Linnarsson's (1883) type material of '*Paradoxides brachyrhachis*' has shown that there are problems in its nomenclature, identification and classification that the present paper aims to resolve. The species is redescribed herein and the differences from the Gondwanan species *Eccaparadoxides mediterraneus* (Pompeckj, 1901) are discussed.

Paradoxides brachyrhachis was described by Linnarsson in 1883, on the basis of material from Andrarum (locality 11 of Tullberg 1880), Scania, southern Sweden. In the same work, he discussed whether some of the specimens identified by Brøgger (1878) as *P. rugulosus* Hawle & Corda, 1847 might be included in his new species. Linnarsson noted that, in spite of being incomplete, the pygidia from Andrarum had a very similar outline and might also originally have had two marginal spines, like those present in Brøgger's specimen (1878, pl. 2, fig. 1a). Regarding the cranidia, only the largest one of those figured by Brøgger (1878, pl. 2, fig. 1) was accepted by Linnarsson as possibly assignable to *P. brachyrhachis*.

Fig. 1. Geographical distribution of the studied specimens (marked by an asterisk). Bo = Bornholm, Denmark, Sa = Sardinia, Italy.

The first identification of '*Paradoxides brachyrhachis* Linnarsson' from the Iberian Peninsula was by Lotze (1958), recording a determination by Sdzuy. Sdzuy (1961) figured this species from Spain for the first time.

Paradoxides mediterraneus was erected by Pompeckj (1901), using material from Sardinia. He included the specimens assigned to *Paradoxides rugulosus* Corda by Bergeron (1889) in the synonymy list. He discussed the differences in the cranidia and thoraces and the similarities in the pygidia of this new species with *P. rugulosus* from Bohemia.

Courtessole (1973, pp. 126, 130), following Sdzuy (1961), remarked that *Paradoxides* (*Eccaparadoxides*) *mediterraneus* and *P. brachyrhachis* are very similar, differing only in the pygidium. They have been considered to represent the same species by some authors (e.g. Liñán & Gozalo 1986).

Systematic palaeontology

Repositories – All specimens described and discussed herein are housed in the collections of the Geological Survey of Sweden, Uppsala (SGU), the Geological Museum, University of Oslo, Norway (PMO), the Geological Museum, University of Copenhagen, Denmark (MGUH), the Museo Paleontológico, University of Zaragoza, Spain (MPZ), the Dipartimento di Scienze della Terra, University of Cagliari, Italy (DSTCP), and the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS).

Terminology – Trilobite descriptive terminology follows Whittington & Kelly *in* Kaesler (1997).

Class Trilobita Walch, 1771

Order Redlichiida Richter, 1932

Superfamily Paradoxidoidea Hawle & Corda, 1847

Family Paradoxididae Hawle & Corda, 1847

Genus *Mawddachites* Fletcher, 2007

Type species. – *Paradoxides hicksii* Salter, 1866 from the Clogau Shales (middle Cambrian) in the Mawddach Valley, North Wales; by original designation.

Mawddachites? brachyrhachis (Linnarsson, 1883)

Fig. 2D–I

Synonymy. – v *non* 1878 *Paradoxides rugulosus* Corda – Brøgger, pp. 39–42, pl. 2, fig. 1, 1a–c (described and figured from Norway).
?1878 *Paradoxides rugulosus* Corda – Brøgger, pp. 39–42, pl. 2, figs. 2, 3 (described and figured).
non 1878 *Paradoxides rugulosus* Corda – Brøgger, pp. 39–42, pl. 2, figs. 4, 4b, c, 5.
v 1883 *Paradoxides brachyrhachis* [also *brachyrrhachis*] n. sp. – Linnarsson, pp. 16–18, pl. 3, figs. 6–10.
v *non* 1902 *Paradoxides rugulosus* Corda – Grönwall, pp. 113–117, pl. 3, figs. 1–4.
1958 *Paradoxides brachyrhachis* Linnarson [sic] – Šnajdr, p. 103 [transfers the species to *Hydrocephalus*].
non 1961 *Paradoxides brachyrhachis* Linnarsson 1883 – Sdzuy, pp. 326–330, pl. 19, figs. 19–21, pl. 20, figs. 1–14, pl. 21, figs. 1–9, text-fig. 27.
non 1964 *Paradoxides brachyrhachis* Linnarson – Meléndez & Asensio Amor, pp. 8–9, pl. 2, fig. A.
non 1970 *Paradoxides brachyrhachis* Linnarsson, 1883 – Gil Cid, pp. 165–166, pl. 1, figs. 2–5, 8–10.
non 1973 *Paradoxides* (*Eccaparadoxides*) *brachyrachis* [sic] Linnarsson 1883 – Courtessole, pp. 126–129, pl. 5, figs. 5–11, pl. 6, figs. 1–7, pl. 7, figs. 1–4, pl. 8, fig. 1 [with reservation], text-fig. 23.4 [listed as 23.3 in the explanation].
non 1982 *Paradoxides* (*Eccaparadoxides*) *brachyrhachis* Linnarsson, 1883 – Gil Cid, pp. 11–12, 14, figs. 1–11.
v *non* 1986 *Paradoxides* (*Eccaparadoxides*) *brachyrhachis brachyrhachis* Linnarsson 1883 – Liñán & Gozalo, pp. 56–58, pl. 16, figs. 12–14, pl. 17, figs. 1–2, pl. 18, figs. 1–9, pl. 19, figs. 1–12, pl. 20, figs. 1–8.
v *non* 1991 *Paradoxides* (*Eccaparadoxides*) *brachyrhachis brachyrhachis* Linnarsson 1883 – Gámez et al., pl., fig. 1.
non 1992 *Paradoxides* (*Eccaparadoxides*) *brachyrachis* [sic] ou *mediterraneus* – Pillet, pl. 1, fig. 1.
non 1992 *Paradoxides* (*Eccaparadoxides*) *brachyrachis* [sic]– Pillet, pl. 1, fig. 2.
non 1992 *Paradoxides* (*Eccaparadoxides*) *mediterraneus* – Pillet, pl. 1, fig. 3.
v *non* 1999 *Eccaparadoxides brachyrhachis* – Álvaro et al., fig. 5J.
v *non* 1999 *Paradoxides* (*Eccaparadoxides*) *brachyrhachis* Linnarsson, 1883 – García-Bellido Capdevilla, pl. 1, figs. 3–4.
v *non* 2003 *Eccaparadoxides brachyrhachis* (Linnarsson, 1883) – Gozalo et al., pl. 3, figs. 7–9, pl. 4, figs. 1–4, text-fig. 6.
v *non* 2008 *Eccaparadoxides brachyrhachis* (Linnarsson, 1883) – Liñán et al., pp. 17, 19, fig. 7, p. 20, p. 40, fig. 20b–c.

Name. – Although Linnarsson (1883) used the spelling *brachyrhachis* where it heads the formal description on p. 16, he used the spelling *brachyrrhachis* elsewhere in his memoir, and there can be no doubt that this latter form is the spelling Linnarsson intended. This was recognised by Grönwall (1902), who used the spelling *brachyrrhachis* in his synonymy of

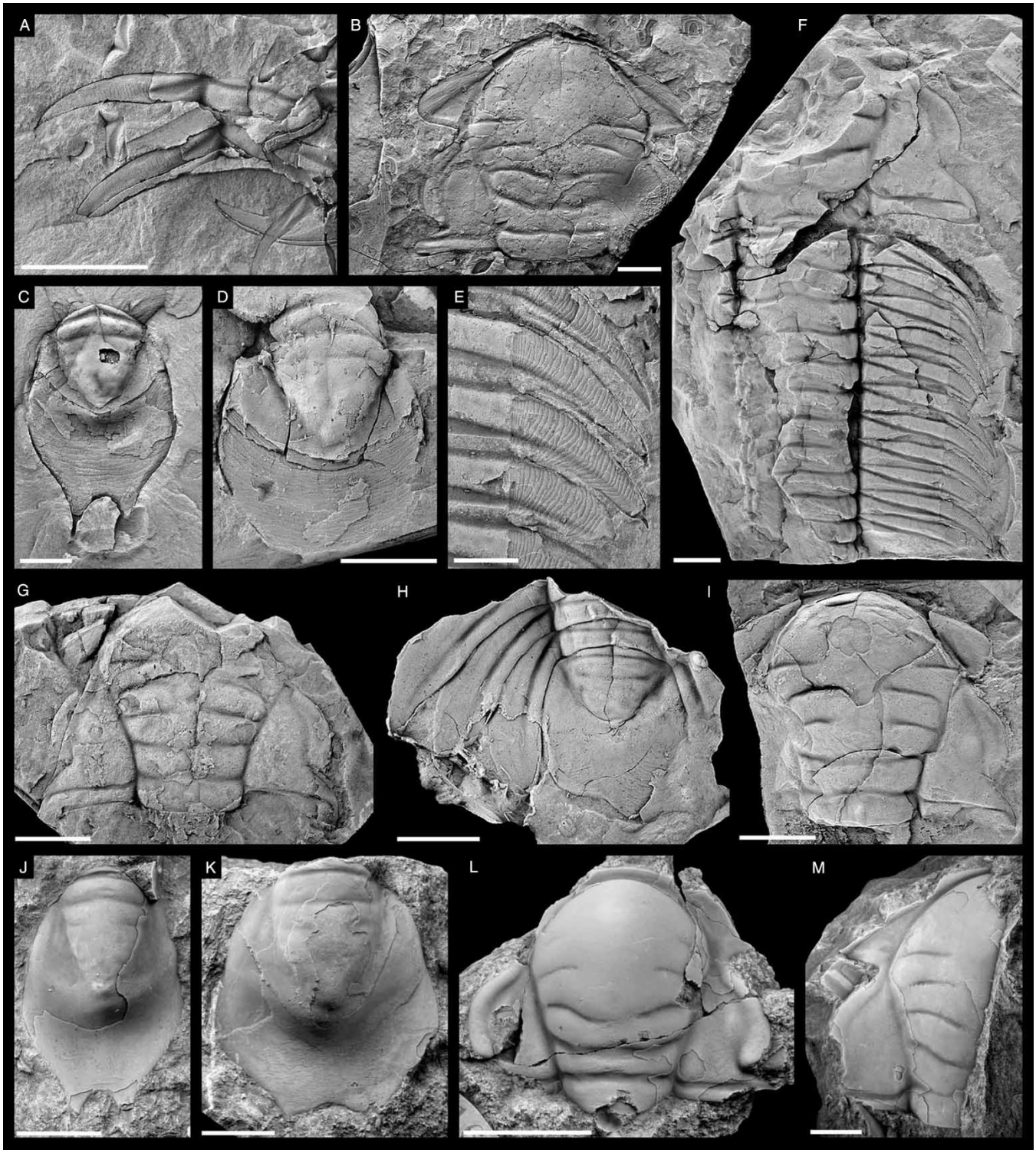

Fig. 2. Paradoxidids from the middle Cambrian of Scandinavia. Whitened with ammonium chloride prior to photography. Scale bar = 1 cm. A–C. '*Paradoxides rugulosus* Hawle & Corda' of Brøgger (1878); middle Cambrian, Krekling, Norway. **A.** Two pleural spines, original of Brøgger (1878, pl. 2, Fig. 4b), PMO 8242. **B.** Cranidium, original of Brøgger (1878, pl. 2, Fig. 2), PMO H2646. **C.** Pygidium, original of Brøgger (1878, pl. 2, Fig. 1a), PMO H2656. D–I. *Mawddachites*? *brachyrhachis* (Linnarsson, 1883); *Ptychagnostus punctuosus* Zone, middle Cambrian, Andrarum, Scania, Sweden; Specimens figured by Linnarsson (1883). **D.** Pygidium, original of Linnarsson (1883, pl. 3, Fig. 10), SGU Type 5582. **E.** Close-up of pleural spines, same specimen as Fig. F. **F.** Incomplete specimen with at least 11 thoracic segments, original of Linnarsson (1883, pl. 3, Fig. 8), SGU Type 5580a. **G.** Incomplete cranidium, original of Linnarsson (1883, pl. 3, Fig. 6), SGU Type 5578. **H.** Latex cast of pygidium with three incomplete thoracic tergites, original of Linnarsson (1883, pl. 3, Fig. 9), SGU Type 5581. **I.** Incomplete cranidium, lectotype, original of Linnarsson (1883, pl. 3, Fig. 7), SGU Type 5579. J–M. '*Paradoxides rugulosus* Corda' of Grönwall (1902); middle Cambrian, Bornholm, Denmark. **J.** Pygidium, original of Grönwall (1902, pl. 3, Fig. 3), MGUH 170. **K.** Pygidium, original of Grönwall (1902, pl. 3, Fig. 4), MGUH 171. **L.** Incomplete cranidium, original of Grönwall (1902, pl. 3, Fig. 2), MGUH 169. **M.** Incomplete cranidium, original of Grönwall (1902, pl. 3, Fig. 1), MGUH 168.

Paradoxides rugulosus. He is, however, not the 'first reviser' in the sense of Article 24.2.3 of the International Code of Zoological Nomenclature (ICZN 1999), because he did not also cite the form '*brachyrhachis*'. We, as first revisers, here select the linguistically more correct spelling *brachyrhachis* as the correct original spelling for Linnarsson's species. The species has been cited as *P. brachyrhachis* by, e.g., Westergård (1953), Šnajdr (1958), Sdzuy (1961), and Liñán & Gozalo (1986), and as *P. brachyrachis* by Courtessole (1973) and Kordule (1990).

Although the title page of Linnarsson's work bears the date 1882, the postscript on the last page of this work is dated 1 March 1883, and this is accepted as the year of publication.

Lectotype. – A cranidium (SGU Type 5579; Fig. 2I), the original of Linnarsson (1883, pl. 3, fig. 7), is selected here as lectotype. Paralectotypes are an incomplete cephalothorax (SGU Type 5580a, b; Linnarsson 1883, pl. 3, fig. 8), a nearly complete cranidium (SGU Type 5578; Linnarsson 1883, pl. 3, fig. 6), a pygidium with three incomplete thoracic tergites (SGU Type 5581; Linnarsson 1883, pl. 3, fig. 9), and a pygidium (SGU Type 5582; Linnarsson 1883, pl. 3, fig. 10).

Material and occurrence. – Linnarsson's (1883) figured specimens were collected by G.C. von Schmalensee from 'shales with *Paradoxides davidis*' at Andrarum, Scania, southern Sweden, and remain the only material known from the type locality. Westergård (1953, p. 36), recorded the species from the *Ptychagnostus punctuosus* Zone (B4) and also, with doubt, from the *Solenopleura*? *brachymetopa* Zone (C2). The latter zone is currently included in the *Lejopyge laevigata* Zone (Axheimer et al. 2006).

The specimens figured from Norway by Brøgger (1878) and from Denmark by Grönwall (1902) have also been examined, and are here excluded from *Mawddachites*? *brachyrhachis* (Linnarsson).

Description. – Cranidium subtrapezoidal in shape. Anterior border flat, much narrower in front of glabella than abaxially. Preglabellar field absent. Glabella slightly convex, widening forward almost evenly to a maximum at the level of S4. Frontal lobe rounded, almost semicircular. Four pairs of glabellar furrows, well marked abaxially. S1 is weakly transglabellar and transverse or arched backwards slightly. S2, S3 and S4 are nearly transverse and long, but not connected across the glabella; S2 and S3 are subparallel, slightly oblique inwards and forwards, whereas S4 is transverse. Glabellar lobes (L1–L4) are subequal in length (exsag.), but L2 is shorter at the axial furrow than adaxially. L3 is nearly rectangular and L4 is longer at the axial furrow than adaxially. Occipital furrow (SO) slightly bent forwards in the axial area and straight abaxially. Occipital lobe (LO) subrectangular, narrower (tr.) than L1, and with an axial node (Fig. 2I). Palpebral lobes diverge backwards from the mid-length of L4 to the mid-length of L1 and do not touch the glabella, about 2/5 of the glabellar length, weakly curved, widening a little from points γ to δ (Fig. 2G, I). Palpebral furrow shallow. Palpebral field of fixigena subtriangular, narrow (trans.) and flat. Postocular field c. 1/2 as long as palpebral field, trapezoidal in shape and as flat as the palpebral field. Posterior furrow deep and narrow. Posterior border rectangular and not quite as wide (exsag.) as the occipital lobe. Posterior margin nearly straight. 'S' parameter (Liñán Guijarro 1978) tangential and strongly convergent forwards. Anterior branch of facial suture short (as long as the width of anterior border), weakly divergent forwards. Posterior branch long, about half as long as the ocular suture, extended backwards and outwards at about 45 degrees, and then curved backwards to the posterior margin.

The most complete thorax has 11 or 12 segments preserved. Axial rings homogeneous (sag.) but slightly bent forwards adaxially. Pleural field slightly wider than axis. Doublure on pleural spines occupying the outer 1/3 (as seen in the anterior segments; Fig. 2F). Thoracic segments end in sharply pointed spines that are curved backwards. Some exfoliated spines show the ventral doublure with terrace lines (Fig. 2E). Pleural furrow long and deep, extending across the inner edge of the doublure and far towards the pleural tips.

Pygidium elongate and subelliptical in outline, so far as known, and widest close to or just behind mid-length. Axis triangular, approximately 1/2 the pygidial length. It shows the anterior axial ring distinctly and a second ring very indistinctly. Posterior part of axis pointed and longer than the two rings combined. Pleural field depressed around the axial furrow and flat abaxially. Anterior pleural furrow weak or absent. Doublure extends forward almost to the posterior of the axis. The posterior outline of the pygidia is not completely preserved, and it is not known whether pygidial marginal spines were developed.

Discussion. – *Mawddachites*? *brachyrhachis* is known only from incomplete cranidia, a part of a thorax and two incomplete pygidia. They differ from *M. hicksii* because the frontal lobe of the glabella is bluntly rounded and less protuberant than in *M. hicksii*, the anterior border is evenly rounded in outline (contrast Fletcher 2007, fig. 8B), the S3 furrow is longer and S4 extends to the axial furrow; the interocular fixigenae do not show the venulose sculpture figured by Fletcher (2007, fig. 8A, B). The pygidia differ from *M. hicksii* in having a shorter, sharply tapered axis and less distinct pleural furrows.

The specimens figured by Brøgger (1878) and doubtfully assigned to *P. brachyrhachis* by Linnarsson (1883) are refigured here for comparison (Fig. 2A–C), as also are Grönwall's (1902) specimens from Bornholm that he considered to be identical to both Brøgger's and to Linnarsson's material (Fig. 2J–M). Grönwall's material may be of the same taxon as Brøgger's, but both differ from Linnarsson's *M.*? *brachyrhachis* in several details: the S1 furrows are connected across the glabella and S2 are longer (tr.); the preocular sutures are more strongly divergent, the anterior border is narrower exsagittally (Fig. 2B) and the preocular genal area behind it is evident, forming a triangle (Fig. 2M); the palpebral lobes are longer, with their posterior ends recurved, and the postocular sutures are shorter and much more divergent (Fig. 2B, L). In Brøgger's cranidium (1878, pl. 2, fig. 1) the S-parameter is exterior and more nearly parallel to the sagittal direction than in Linnarsson's type cranidia (Fig. 2G, I).

The thoracic segments in Brøgger's material (Fig. 2A) have a shorter (tr.) and broader pleural furrow than those of *M.*? *brachyrhachis*. The pygidia illustrated by Brøgger and Grönwall (Fig. 2C, J, K) all show a pair of marginal spines; there is no evidence for similar spines in Linnarsson's specimens, which are, however, imperfectly preserved posteriorly (Fig. 2D, H). In Linnarsson's pygidia the pleural field is fairly flat, but in the spinose form (Fig. 2C, J, K) the pleural field forms a slightly elevated platform anteriorly, and posteriorly, where the ventral doublure is developed, it is depressed relative to the anterior part and may show terrace lines (Fig. 2C). These specimens figured by Brøgger and Grönwall are not considered to be referable to

Mawddachites, but show some resemblance to the Bohemian species *Hydrocephalus lyelli* (Barrande, 1852), redescribed by Šnajdr (1958, p. 141, pl. 17, figs. 2, 3, pl. 18, figs. 3–6, pl. 19, figs. 1–14), and subsequently transferred to *Rejkocephalus* by Kordule (1990). In *R. lyelli* the S3 and S4 furrows tend to be weaker and shorter, the palpebral lobe is shorter and the postocular suture longer. The pygidium of *R. lyelli* has 1–2 pairs of well-marked pleural furrows. Another comparable species is the rather poorly known *Paradoxides freboldi* Hutchinson, 1962. Hutchinson's (1962) holotype, a large fragmentary cranidium, is quite like our Fig. 2M, though the preocular suture is less divergent and the palpebral lobe is thicker. Hutchinson's two pygidia show a wide and a narrow form, just like our Fig. 2J, K, but differ in having a well-marked pleural furrow and a shorter post-axial field.

Generic position. – The generic or subgeneric status of many paradoxidids is a matter of some uncertainty. Although *P. mediterraneus* is appropriately referred to *Eccaparadoxides* (here treated as of generic rank) because it is similar to the type species *E. pusillus* (Barrande, 1846), *P. brachyrhachis* was placed in the same genus only because of its supposed similarity to *E. mediterraneus.* However, the form of the glabella in Linnarsson's material, the longer postocular suture, the shorter palebral lobes, and the narrowing of the frontal border medially where it is in contact with the glabella, are not typical of *Eccaparadoxides.* Šnajdr (1958) placed *P. brachyrhachis* in *Hydrocephalus* (type species *H. carens* Barrande, 1846) but we observe that in glabellar features *brachyrhachis* is more similar to *P. lyelli* Barrande, 1852 and *Paradoxides hicksii* Salter, 1866. Of these species, *P. lyelli* was referred by Kordule (1990) to *Rejkocephalus* (type species *P. rotundatus* Barrande, 1846), and Fletcher (2007, p. 47) has made *P. hicksii* the type species of a new subgenus *Paradoxides* (*Mawddachites*). A cladistic study by Mark Bell and Adrian Rushton (in preparation) shows that a group of species, including *Paradoxides hicksii*, form a small clade, appropriately referred to *Mawddachites* Fletcher, 2007, and treated here as a genus. In this analysis Linnarsson's *P. brachyrhachis* is sister to species of *Mawddachites*, so we place *P. brachyrhachis* provisionally in the same genus.

Genus *Eccaparadoxides* Šnajdr, 1957

Type species. – *Paradoxides pusillus* Barrande, 1846 from the lower Jince Formation (middle Cambrian) of Bohemia; by original designation.

Eccaparadoxides mediterraneus (Pompeckj, 1901)

Figs 3A–G, 4A–I, 5A–D

Synonymy. – 1889 Paradoxides rugulosus – Bergeron, p. 336, pl. 2, figs. 5–7.
v 1901 Paradoxides mediterraneus n. sp. – Pompeckj, pp. 2–4, pl. 1, figs. 1–3.
1926 Paradoxides mediterraneus – Lecointre, p. 108, pl. 12, figs. 5–7.
v 1935 Paradoxides spinosus Boeck – Sampelayo, pl. 15, fig. 2.
v 1935 Paradoxides barrandei Barrois – Sampelayo, pl. 16, fig. 1.
v 1935 Paradoxides rotudantus Barrande – Sampelayo, pl. 17, fig. 2.
v 1935 Paradoxides rugulosus Corda – Sampelayo, pl. 17, fig. 4.
1943 Paradoxides spinosus Boeck – Meléndez, pl. 17.
1959 Paradoxides rotundatus Barrande – Badillo, pl. 47.
1959 Paradoxides rugulosus Corda – Badillo, pl. 49.
v 1961 Paradoxides brachyrhachis Linnarsson 1883 – Sdzuy, pp. 326–330, pl. 19, figs. 19–21, pl. 20, figs. 1–14, pl. 21, figs. 1–9, text-fig. 27.
1961 Paradoxides mediterraneus Pompeckj 1901 – Sdzuy, pp. 330–331, pl. 21, figs. 10–12, text-fig. 28.
1964 Paradoxides spinosus Boeck – Meléndez & Asensio Amor, pp. 6–7, pl. 1, figs. A, D.
1964 Paradoxides bohemicus Boeck – Meléndez & Asensio Amor, pp. 7–8, pl. 1, figs. B, C.
1964 Paradoxides brachyrhachis Linnarson – Meléndez & Asensio Amor, pp. 8–9, pl. 2, fig. A.
1970 Paradoxides brachyrhachis Linnarsson, 1883 – Gil Cid, pp. 165–166, pl. 1, figs. 2–5, 8–10.
1970 Paradoxides mureroensis Sdzuy, 1958 – Gil Cid, pl. 1, fig. 6–7, 12–13.
?1972 Paradoxides cf. mediterraneus Pompeckj – Rasetti, pp. 62–63, pl. 17, fig. 15.
?1972 Paradoxides, sp. indet. – Rasetti, p. 63, pl. 17, figs. 11–14.
1973 Paradoxides (Eccaparadoxides) brachyrachis [sic] Linnarsson 1883 – Courtessole, pp. 126–129, pl. 5, figs. 5–11, pl. 6, figs. 1–7, pl. 7, figs. 1–4, pl. 8, fig. 1 [with reservation], text-fig. 23.4 [listed as 23.3 in the explanation].
1973 Paradoxides (Eccaparadoxides) mediterraneus (Pompeckj 1901) – Courtessole, pp. 130–131, pl. 7, figs. 5–9, pl. 8, fig. 1, text-fig. 23.3.
v 1982 Paradoxides (Ecc.) mediterraneus? – Palacios, pp. 46–47, pl. 4, figs. 6–11.
v 1986 Paradoxides (Eccaparadoxides) brachyrhachis brachyrhachis Linnarsson, 1883 – Liñán & Gozalo, pp. 56–58, pl. 16, figs. 12–14, pl. 17, figs. 1–2, pl. 18, figs. 1–9, pl. 19, figs. 1–12, pl. 20, figs. 1–8.
v 1991 Paradoxides (Eccaparadoxides) brachyrhachis brachyrhachis Linnarsson, 1883 – Gámez et al., pl., fig. 1.
1992 Paradoxides (Eccaparadoxides) brachyrachis ou mediterraneus – Pillet, pl. 1, fig. 1.
1992 Paradoxides (Eccaparadoxides) brachyrachis – Pillet, pl. 1, fig. 2.
1992 Paradoxides (Eccaparadoxides) mediterraneus – Pillet, pl. 1, fig. 3.
v 1994 Paradoxides mediterraneus – Pillola, fig. 8.
v 1995 Paradoxides (Eccaparadoxides) mediterraneus (Pompeckj 1901) – Loi et al., pl. 4, fig. 23.
v 1999 Eccaparadoxides brachyrhachis Linnarsson, 1883 – Álvaro et al., fig. 5J.
v 1999 Paradoxides (Eccaparadoxides) brachyrhachis Linnarsson, 1883 – García-Bellido Capdevilla, pl. 1, figs. 3–4.
v 2003 Eccaparadoxides brachyrhachis (Linnarsson, 1883) – Gozalo et al., pl. 3, figs. 7–9, pl. 4, figs. 1–4, text-fig. 6.
v 2008 Eccaparadoxides brachyrhachis (Linnarsson, 1883) – Liñán et al., pp. 17, 19, 20 40, figs. 7, 20b, c.

Lectotype. – All syntypes, except an almost complete but distorted specimen, were lost during World War II. The surviving specimen (Pompeckj 1901, pl. 1, fig. 1, SMNS 21382; here Fig. 3A) is selected here as lectotype. It is from the base of the Cabitza Formation at Iglesias, Sardinia.

Material. – From Sardinia: 12 complete specimens, 32 articulated but damaged exoskeletons lacking the posterior or the anterior part, generally with the librigenae attached, 8 cranidia, 2 isolated librigenae, 10 pygidia, and 3 incomplete

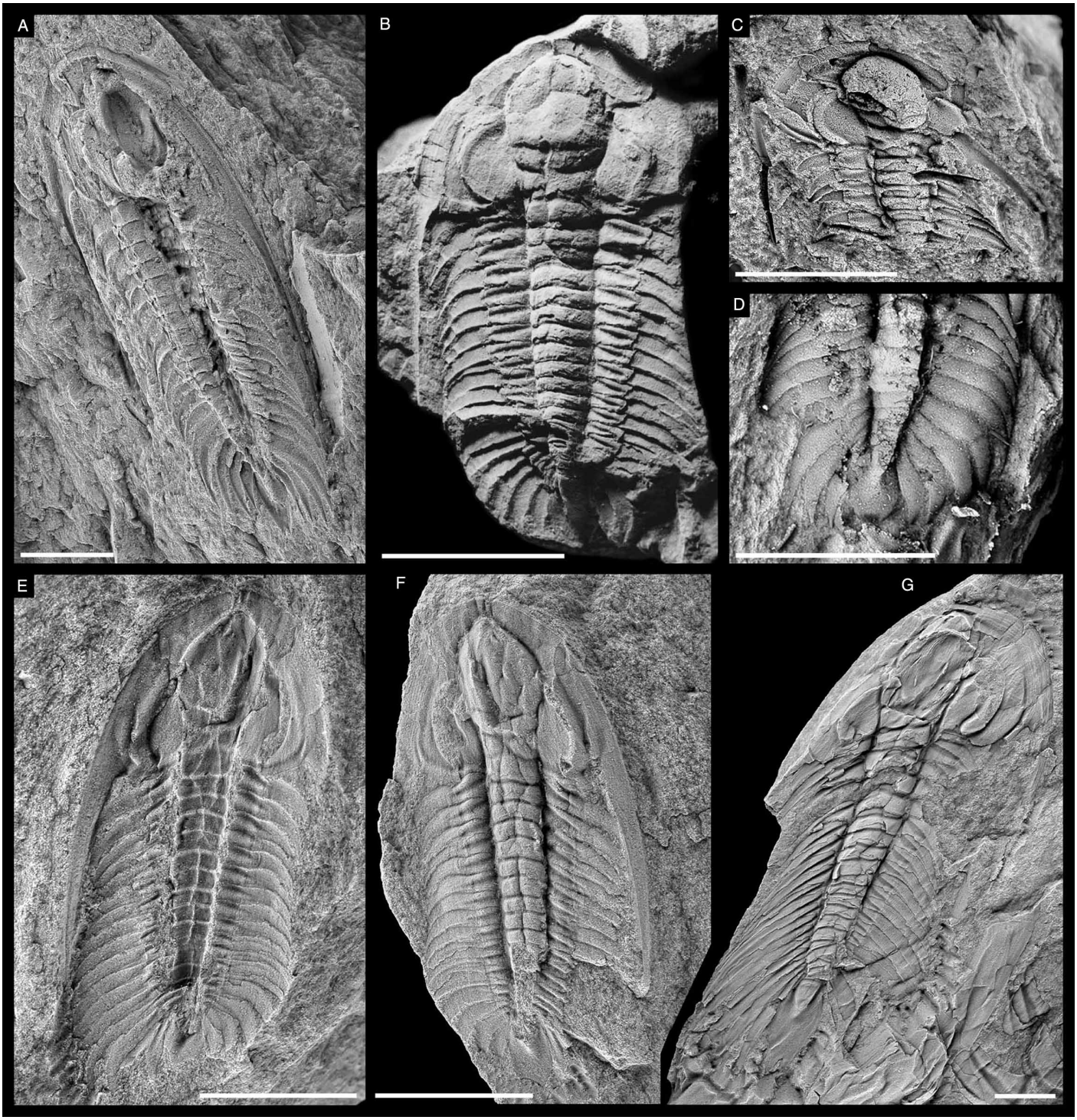

Fig. 3. Eccaparadoxides mediterraneus (Pompeckj, 1901). Whitened with ammonium chloride prior to photography. Scale bar = 1 cm. A–D. Base of the Cabitzia Formation (middle Cambrian), Sardinia. **A.** Lectotype, an almost complete articulated specimen, SMNS 21382. **B.** Internal mould of a nearly complete specimen, type section (Iglesias), DSTCP 22483. **C.** Incomplete articulated specimen, internal mould blackened with china ink and whitened with ammonium chloride, Pertunto (Carbonia), DSTCP. 22782. **D.** Close-up of posterior portion of a complete specimen, latex cast, Pertunto (Carbonia). DSTCP. 22781. E–G. Murero Formation (middle Cambrian); Mesones area, Iberian Chains, Spain. **E.** Articulated complete specimen, external mould, MPZ 2009/354. **F.** Articulated complete specimen, internal mould, MPZ 2009/354. **G.** Articulated almost complete specimen, internal mould, MPZ 2009/355.

thoraces. The material is preserved as limonitic and/or chloritic yellowish-greenish internal moulds and counterparts in fine siltstones and decalcified marlstones.

From the Iberian Chains: 11 complete specimens, 300 cranidia, 20 librigenae, 4 rostral plates, 35 pygidia, 11 hypostomes, and 6 incomplete thoraces. They are preserved as limonitized and

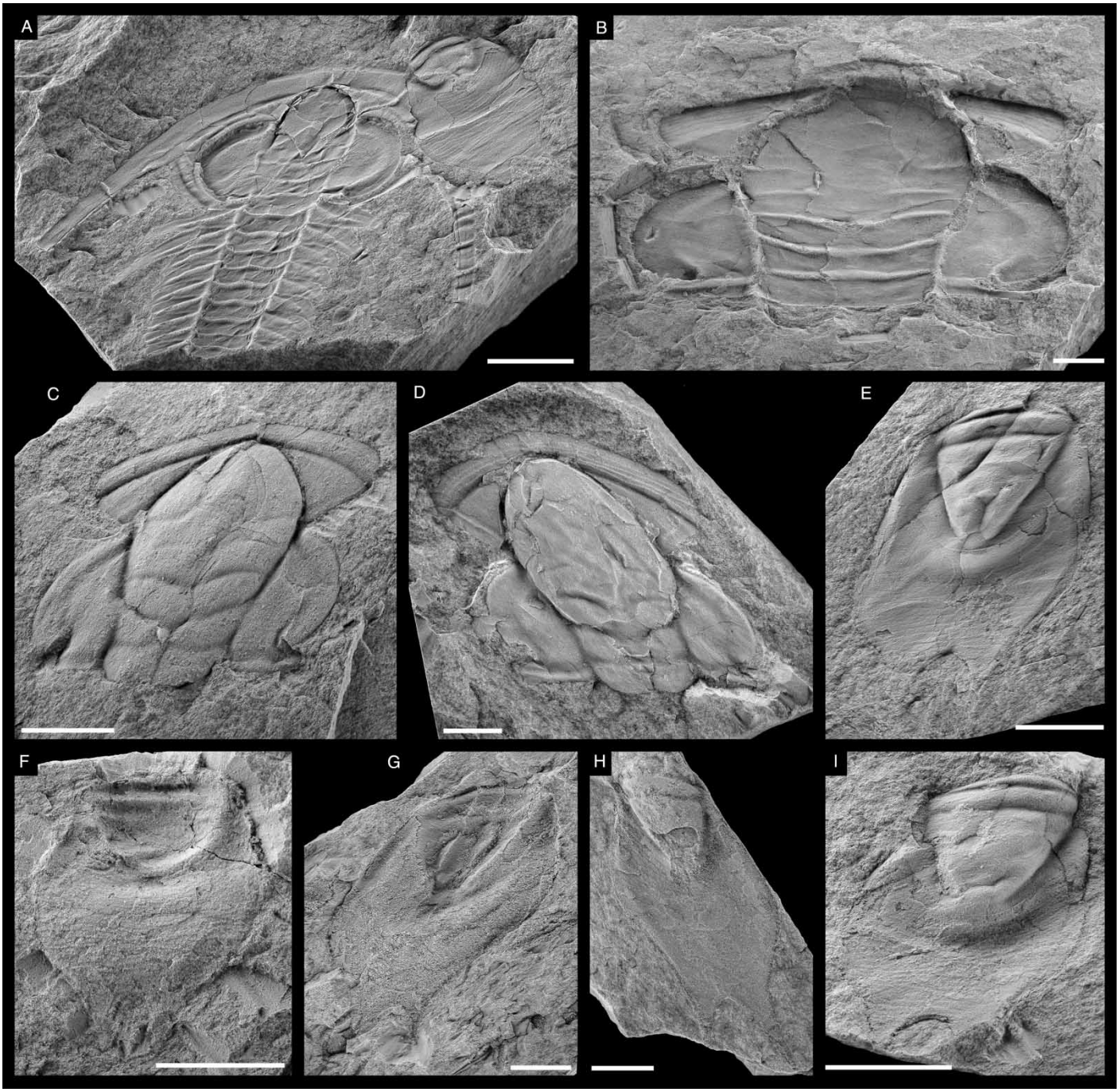

Fig. 4. Eccaparadoxides mediterraneus (Pompeckj, 1901). Murero Formation, Spain. Whitened with ammonium chloride prior to photography. Scale bar = 1 cm. **A**. Internal mould of cephalon with 9 thoracic segments, partially covered by a pygidium, Mesones area, MPZ 2009/349. **B.** External mould of cranidium, Murero area, MPZ 3006. **C.** Internal mould of cranidium, Murero area, MPZ 2009/352. **D.** Internal mould of cranidium, Murero area, MPZ 3014. **E.** Internal mould of pygidium, Mesones area, MPZ 2009/356. **F.** External mould of pygidium, Mesones area, MPZ 2009/351. **G.** External mould of pygidium, Murero area, MPZ 2009/350. **H.** Internal mould of pygidium, Mesones area, MPZ 2009/353. **I.** Internal mould of pygidium, Mesones area, MPZ 2009/357.

chloritized internal moulds and counterparts in lutites and fine-grained sandstones.

All specimens have suffered tectonic deformation to some degree.

Description. – Cephalon elliptical in shape. Cranidium subrectangular with curved anterior margin. Anterior border flat, only slightly narrower in front of the glabella and with terrace lines parallel to the anterior margin. Anterior furrow deep. Preglabellar field absent. Glabella pyriform, convex and with four pairs of lateral glabellar furrows. S1 and S2 well marked and transglabellar, S1 curved backwards, S2 transverse or slightly curved backwards. S3 and S4 shallow and not transglabellar, almost transverse or slightly forwardly arched medially. Frontal lobe of glabella semicircular. L1 becomes

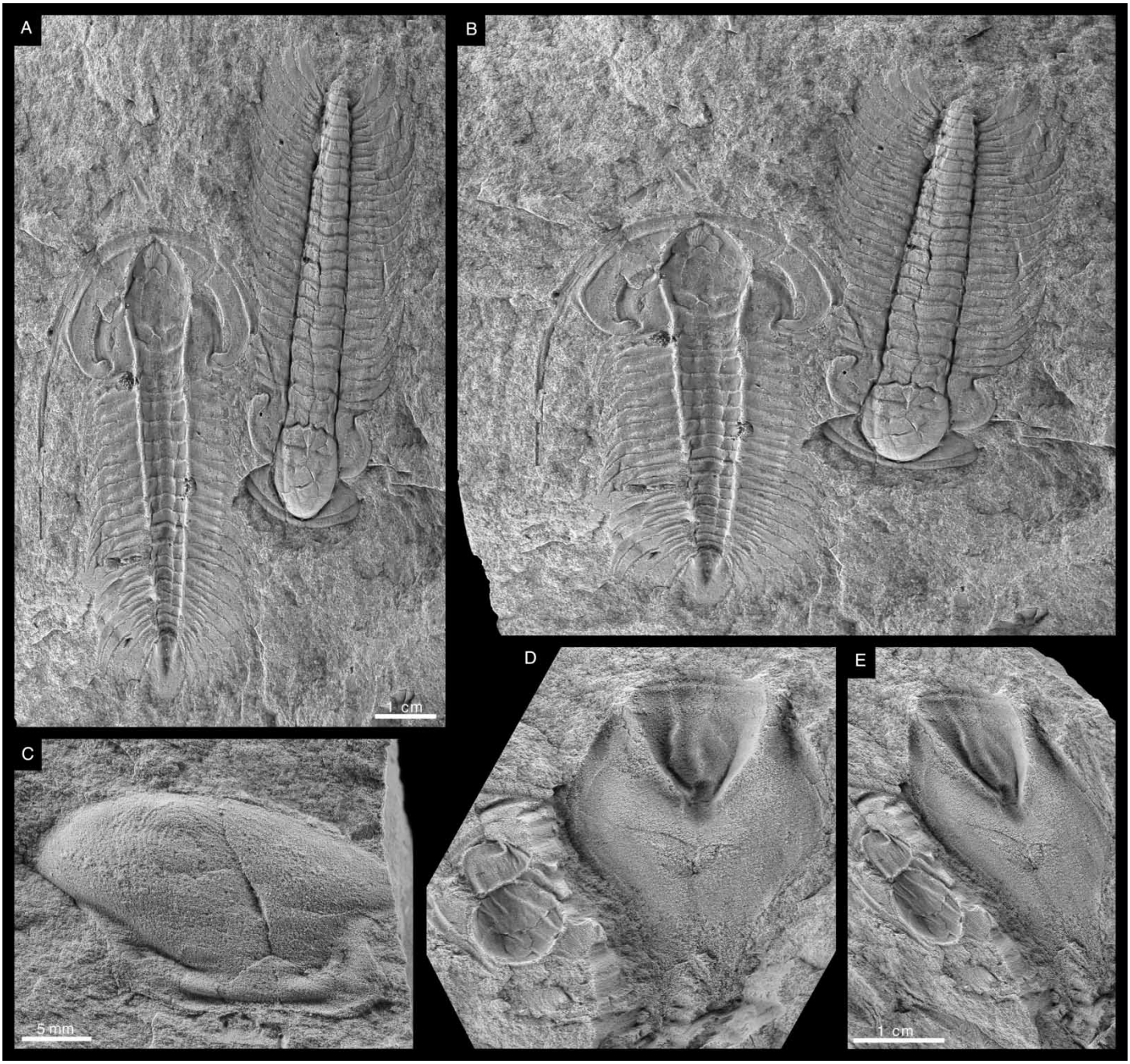

Fig. 5. Eccaparadoxides mediterraneus (Pompeckj, 1901). Murero Formation, Spain. Whitened with ammonium chloride prior to photography. **A.** Two complete specimens, external mould (left) and internal mould (right), Murero area, MPZ 3004. **C.** Internal mould of hypostome, Murero area, MPZ 3032. **E.** Pygidium and cranidium, external moulds, Murero area, MPZ 2009/348. **B, D.** Specimens figured in A and E after retrodeformation following the methods of Cooper (1990). The eccentricity of the strain ellipse, R, is 1:1.7.

slightly shorter axially; L2 gently arched backwards (Fig. 4B, C); L4 and L3 transverse, of subequal length (exsag.). Occipital furrow deep, the mid-part arched forward axially. Occipital lobe subrectangular, lengthens adaxially. Preocular field triangular, smooth and flat. Palpebral lobe long, arched, convex, slightly widened in its middle part, connected to glabella between S3 and S4, and reaching or almost reaching the posterior furrow (Fig. 4B). Palpebral area of fixigena semicircular and flat. Posterior border furrow straight, wide and deep. Posterior border rectangular and narrow. *S* parameter (Liñán Guijarro 1978) secant and slightly convergent. It is useful to note that this parameter remains valid even in deformed specimens (Fig. 5A, B).

Librigena wide. Lateral border flat, widening towards the genal spine, and with terrace lines parallel to the lateral margin. Lateral border furrow deep. Lateral surface flat and wider than the lateral border (Fig. 5B). Posterior border oblique to the axis inwards and backwards. Genal angle obtuse, inner spine angle acute. Genal spine long (reaching the 8th thoracic segment), commencing in front of the posterior border.

Hypostome swollen, consisting mainly of the anterior lobe of the middle body, and with terrace lines forming an elongate oval

whorl on the middle body. Hypostomal suture curved. Posterior lobe of middle body narrow. Posterior margin straight and provided with two small spines.

Thorax (including pleural spines) uniformly wide, consisting of 18 segments. Axial rings rectangular. Pleural furrow deep, dividing the pleura into two triangular pleural bands; it is short, extending outwards to the edge of the doublure, beyond which it fades. The two anterior pleurae show elongated pleural spines (macropleural). The third thoracic segment has a shorter pleural spine (micropleural). The fourth to eighteenth pleural segments are uniform in some of the specimens (morphotype A) and micropleural until segment nine in others (morphotype B; for a discussion of morphotypes in *Eccaparadoxides mediterraneus*, see Gozalo et al. 2003). The pleural spines are increasingly curved backwards so that the three to five most posterior spines reach beyond the pygidium.

Pygidium long, subhexagonal in shape, with two more or less well developed spines. Articulating half-ring short. Rachis triangular in shape, with one rectangular and well developed axial ring and a faint furrow indicating the presence of a second ring. Posterior margin of rachis fades into the flat and smooth pleural field. The pygidium is widest just posterior to the end of the rachis. There are two morphotypes of the pygidia, corresponding to morphotypes A and B of the thorax (see above). The ratio of rachial length/pygidial length is $>1/2$ in type A and $<1/2$ in type B.

Occurrence. – Iglesiente-Sulcis, southwest Sardinia, Italy: outcrops at the type locality close to the Cabitza abandoned railway station (Iglesias), Gutturu Pala (Fluminimaggiore), Su Corovau (Domusnovas), Monte Pertunto (Carbonia), Monte Scorra, Monte Agruxiau, and Masua (Iglesias); Villaggio Norma and Monte Onixeddu (Gonnesa), Carbonia-Iglesias Province.

Base of the Cabitza Formation (Iglesias Group); informal assemblage zones CAB 1(?), CAB 2 and CAB 3 (see Pillola et al. 2002 and references therein); middle Cambrian, corresponding to the upper Caesaraugustan to lowermost Languedocian of the Iberian/Mediterranean chronostratigraphy.

Iberian Chains, northeast Spain: Murero, Badules, Ateca, Jarque, Purujosa and Mesones (Zaragoza province) and Borobia (Soria province); Murero and base of Borobia formations. Cantabrian Mountains, northwest NW Spain: Los Barrios de Luna, Genestosa and Vegadeo (León province), and Concha de Artedo (Asturias). In both areas the species is found in the *Solenopleuropsis riberoi–S. verdiagana* Zone to the *S. thorali* Zone (upper Caesaraugustan to lowermost Languedocian; middle Cambrian).

Montagne Noire, southern France: Levels B to F in the Ravin du Brian and Couloma sections (upper Caesaraugustan to lowermost Languedocian; middle Cambrian).

In addition, Lecointre (1926) figured and described some specimens from the Cambrian of the Casablanca area, Morocco.

Discussion. – Compared to *Mawddachites*? *brachyrhachis*, *Eccaparadoxides mediterraneus* has a more developed preocular fixigenal field than *M*.? *brachyrhachis*, in which the preocular field is almost absent, and longer and more arcuate palpebral lobes.

Eccaparadoxides mediterraneus is more similar to the Bohemian species *E. pusillus* (Barrande 1846), which is also recorded from Sardinia (CAB.2 informal zone). In this species, the preocular field is almost as much reduced as in *M*.? *brachyrhachis*. The palpebral field is wider than in both *M. brachyrhachis* and *E. mediterraneus*, and also than in the specimens figured by Brøgger and Grönwall. In addition, *E. pusillus* shows a finely granulose carapace.

In the thorax figured by Linnarsson (1883) the pleural furrow almost reaches the pleural spine tip (Fig. 2E), whereas in *E. mediterraneus* the furrow fades at the beginning of the pleural spine (Figs. 3, 4A, 5A).

The similarity in the pygidia attributed to *M. brachyrhachis* and *E. mediterraneus* probably explains why specimens of the latter species were assigned to the former. However the retrodeformation carried out on some of the specimens (Fig. 5) shows that the lateral outline of the pygidia is clearly different. In the Scandinavian specimens formerly attributed to *P. brachyrhachis*, the outline is uniformly curved, almost elliptical (Figs. 2C, J, K), whereas it is almost hexagonal in the Mediterranean ones (Figs. 5D, E). Another difference between these species can be observed in the pygidial rachis: in *E. mediterraneus*, the pygidial rachis fades into the pleural surface, while it is more clearly defined posteriorly in *M. brachyrhachis*. The pygidium in *Eccaparadoxides pusillus* does not show a distinct pair of spines, but it has an invaginated posterior margin with obtuse points posterolaterally and a more rounded shape.

Conclusions

The revision of Linnarsson's type material of *Paradoxides brachyrhachis* has led us to reject the records of this species in southern Europe, and we assign specimens identified as *P. brachyrahchis* from Spain, Sardinia and France to *Eccaparadoxides mediterraneus.* The type material of the species *P. brachyrhachis* is tentatively assigned to the genus (or subgenus) *Mawddachites* Fletcher, 2007.

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