



The nomenclatural status of
***Palaeothrissum inaequilobum* BLAINVILLE, 1818,**
***P. parvum* BLAINVILLE, 1818, and *Aeduella blainvillei* (AGASSIZ, 1833)**
(Actinopterygii, Aeduellidae)

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Abstract: It is shown that the species names *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818, from the Lower Permian (Asselian) of Muse, near Autun (Saône-et-Loire department, France) are senior synonyms of the widely used species name, *Aeduella blainvillei* (AGASSIZ, 1833). In the interest of nomenclatural stability, conditions exist which allow reversal of precedence as stated in Article 23.9.1 of the International Code of Zoological Nomenclature. Thus the species name *Aeduella blainvillei* (AGASSIZ, 1833) is regarded as valid, qualifying as a *nomen protectum*, whereas *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818, are invalid, qualifying as *nomina oblita*. Some of the specimens from the type series upon which *P. inaequilobum*, *P. parvum* and *Aeduella blainvillei* were erected, are identified.

Key-words:

- Aeduellidae;
- *Aeduella*;
- Permian;
- Asselian;
- Autunian;
- reversal of precedence

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Résumé : **Statut nomenclatural de *Palaeothrissum inaequilobum* BLAINVILLE, 1818, *P. parvum* BLAINVILLE, 1818, et *Aeduella blainvillei* (AGASSIZ, 1833) (*Aeduelliformes*, *Aeduellidae*).** - Il est montré que les noms spécifiques *Palaeothrissum inaequilobum* BLAINVILLE, 1818, et *P. parvum* BLAINVILLE, 1818, du Permien inférieur (Assélien) de Muse, près d'Autun (Saône-et-Loire, France) sont des synonymes plus anciens de l'espèce largement utilisée, *Aeduella blainvillei* (AGASSIZ, 1833). Afin de maintenir la stabilité nomenclaturale, les conditions sont cependant réunies pour une inversion de préséance en accord avec l'article 23.9.1 du Code International de Nomenclature Zoologique. Le nom spécifique *Aeduella blainvillei* est ainsi considéré comme valide et est qualifié de *nomen protectum*, alors que *Palaeothrissum inaequilobum* BLAINVILLE, 1818, et *P. parvum* BLAINVILLE, 1818, sont invalides et qualifiés de *nomina oblita*. Quelques spécimens des séries types sur lesquelles furent créées les espèces *P. inaequilobum*, *P. parvum* et *Aeduella blainvillei*, sont identifiés.

Mots-clefs :

- Aeduellidae ;
- *Aeduella* ;
- Permien ;
- Assélien ;
- Autunien ;
- inversion de préséance

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1. Introduction

Muse (Saône-et-Loire department, France), near Autun, is a well-known Lower Permian vertebrate-bearing fossiliferous site (GAND *et al.*, 2011, 2017). The Muse Formation is part of the regional continental Autunian stratotype that corresponds to the Asselian stage (FALCONNET, 2014). The history of the early fossil fish discoveries in this locality has recently been detailed (BRIGNON, 2014). In 1818, Henri-Marie DUCROTAY de BLAINVILLE (1818a, p. 321; 1818b, p. 17) was the first to describe, without illustration, two new species of fossil fishes from the surroundings of Autun. These species, *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818, were accompanied by brief descriptions and are available according to Articles 11 and 12.1 of the International Code of Zoological Nomenclature (ICZN, 1999). They were based upon specimens in the collections of Barthélémy FAUJAS de SAINT-FOND (1741-1819) and Alexandre BRONGNIART (1770-1847). In the same publication, BLAINVILLE (1818a, p. 393; 1818b, p. 89) indicated that all the specimens were collected in Muse by Cyprien Prosper BRARD (1786-1838) and François-Joseph LAINÉ (1778-1836). The latter reported that the first fishes from Muse were discovered in 1811 (BRIGNON, 2014).

Thereafter, in the first "livraison" of his "Recherches sur les poissons fossiles", AGASSIZ (1833) introduced three new species of fossil fishes from Muse, namely *Palaeoniscum blainvillei*, *Palaeoniscum voltzii* and *Palaeoniscum angustum*, assigning them to the genus *Palaeoniscus* BLAINVILLE, 1818, with the incorrect subsequent spelling *Palaeoniscus* (ICZN, 1999, article 33.3). In his original description, AGASSIZ (1833) explicitly synonymized *Palaeoniscum blainvillei* with *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *Palaeothrissum parvum* BLAINVILLE, 1818. Although the two latter names are objective senior synonyms of the first one, WESTOLL (1937) retained *Palaeoniscum blainvillei* as the type species by monotypy of his newly erected genus *Aeduella*. Since then, *Aeduella blainvillei* (AGASSIZ, 1833) has been considered as valid despite the priority of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *Palaeothrissum parvum* BLAINVILLE, 1818. This paper aims at clarifying this nomenclatural issue.

2. Historical overview

In addition to *Palaeothrissum inaequilobum* and *Palaeothrissum parvum*, BLAINVILLE (1818a, 1818b) also placed in the genus *Palaeothrissum* two other species, *P. macrocephalum* BLAINVILLE, 1818, and *P. magnum* BLAINVILLE, 1818, both from the Kupferschiefer (Upper Permian) of Germany. AGASSIZ (1833, vol. 2, p. 5) showed that *Palaeothrissum macrocephalum* was a subjective synonym of *Palaeoniscum freieslebeni* BLAINVILLE,

1818. As outlined in the introduction, AGASSIZ (1833, vol. 2, p. 4) placed *Palaeothrissum inaequilobum* and *Palaeothrissum parvum* in the genus *Palaeoniscum* BLAINVILLE, 1818. AGASSIZ (1833, p. 10) noted that *Palaeothrissum magnum* BLAINVILLE, 1818, should not be confused with *Palaeoniscum magnum* AGASSIZ, 1833, erroneously written *Palaeoniscus magnus* by AGASSIZ (1833, vol. 2, p. 5; 1834, vol. 2, p. 78-80), a species also from the Upper Permian of Germany. He stated that *Palaeothrissum magnum* BLAINVILLE, 1818, belongs to his newly erected genus, *Pygopterus* AGASSIZ, 1833. As the first reviser, AGASSIZ established that the genus *Palaeothrissum* is a synonym of *Palaeoniscum* (AGASSIZ, 1833, vol. 2, p. 4; WOODWARD, 1891).

In his Handbuch der Petrefaktenkunde, QUENSTEDT (1852, p. 225) gave priority to "*Palaeoniscus*" *inaequilobus* over "*Palaeoniscus*" *blainvillei*. Considering *Palaeoniscum blainvillei* to be a valid name, TRAQUAIR (1877) suggested that this species may be the type of yet another genus. Later, SAUVAGE (1890) restored the priority of the species name "*Palaeothrissum*" *inaequilobum* over *Palaeoniscum blainvillei* and assigned the former to the genus *Amblypterus* AGASSIZ, 1833. According to SAUVAGE, the new combination *Amblypterus inaequilobum* (BLAINVILLE, 1818) included the objective junior synonym *Palaeoniscum blainvillei* and the subjective synonym "*Palaeothrissum*" *parvum* BLAINVILLE, 1818. Sauvage also transferred *Palaeoniscum voltzii* AGASSIZ, 1833, and *Palaeoniscum angustum* AGASSIZ, 1833, to the genus *Amblypterus* AGASSIZ, 1833, considering both species to be valid. However, WOODWARD (1891) rejected the species "*Palaeothrissum*" *inaequilobum* BLAINVILLE, 1818, and "*P.*" *parvum* BLAINVILLE, 1818, arguing that they were inadequately defined. Consequently, WOODWARD retained the species *Amblypterus blainvillei* (AGASSIZ, 1833) and *Amblypterus voltzii* (AGASSIZ, 1833), with the incorrect spelling, *A. voltzi* (ICZN, 1999, article 33.4). He also suggested that *Palaeoniscum angustum* AGASSIZ, 1833, was a juvenile form of *Amblypterus voltzii*.

After the creation of the genus *Aeduella* and the assignment of *Palaeoniscum blainvillei* (AGASSIZ, 1833) as its type species by WESTOLL (1937), the name has been widely accepted. HEYLER (1969) later shown that *Amblypterus voltzii* (AGASSIZ, 1833), *Amblypterus angustus* (AGASSIZ, 1833) and *Palaeoniscum landriotti* SAUVAGE, 1890, were all subjective synonyms of *Aeduella blainvillei* (AGASSIZ, 1833). The stratigraphic and geographic distribution of *Aeduella blainvillei* extends from the Upper Carboniferous (Pennsylvanian) to the Lower Permian (Cisuralian) of France, the Czech Republic, Germany and possibly Switzerland (POPLIN & DUTHEIL, 2005). Emended diagnoses of the species have been published by HEYLER (1969) and POPLIN & DUTHEIL (2005).



Figure 1: A and C: syntypes of *Palaeothrissum inaequilobum* BLAINVILLE, 1818 [*nomen oblitum*], from Muse, "Autunian" continental stratotype (= Asselian), Alexandre BRONGNIART's collection; A, SU.PAL.2017.0.1.16; B, detail of the label written by BRONGNIART "*Palaeothrissum inaequilobum* BL. [BLAINVILLE] *Poiss. Foss. p. 17. sp. [species] 4. Muse près d'Igornay | 2 l. [lieues] au n. [nord] d'Autun*" in reference to BLAINVILLE (1818b); C, MNHN.F.AUT25; D, detail of the label written by BRONGNIART "*Palaeothrissum parvum* BLAINV. [BLAINVILLE] *Poiss. Foss. p. 17. sp. 5. Muse près d'Igornay | 2 l. [lieues] au n. [nord] d'Autun*" in reference to BLAINVILLE (1818b). E, drawing from the CUVIER archives (Bibliothèque centrale du MNHN, Ms 540/10) showing the counterpart of the two previous specimens (credit: © Muséum National d'Histoire Naturelle, Paris). The slab depicted in the drawing was in the collection of BARTHÉLÉMY FAUJAS de SAINT-FOND (1741-1819). Scale bar (A, C): 30 mm.

3. Type series of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818

Two specimens labelled "*Palaeothrissum inaequilobum* BL. [BLAINVILLE]" and one specimen labelled "*Palaeothrissum parvum* BL. [BLAINVILLE]" from the former BRONGNIART collection are kept in the collections of the Muséum national d'histoire Naturelle, Paris (MNHN) (BRIGNON, 2014). The labels in BRONGNIART's hand indicate that they are from Muse, near Autun. MNHN.F.AUT676 (former BRONGNIART collection number 12890) and MNHN.F.AUT704 (former number 12886), on one hand, and MNHN.F.AUT25, (former number 12888), on the other, were therefore presumed

to be syntypes of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818, respectively. Interestingly, a drawing of a slab from Muse bearing two fish specimens in the FAUJAS de SAINT-FOND's collection was rediscovered in the archives of Cuvier curated in the Bibliothèque centrale of the MNHN (Fig. 1.E) (BRIGNON, 2014). One of the depicted specimens (Fig. 1.E, below) is the counterpart of MNHN.F.AUT25 (Fig. 1.C-D), meaning that FAUJAS de SAINT-FOND and BRONGNIART shared parts and counterparts of the same specimens. FAUJAS de SAINT-FOND died in 1819, so that MNHN.F.AUT25 was discovered before 1819 and can confidently be regarded as one of the syntypes of *Palaeothrissum parvum* BLAINVILLE, 1818.



The palaeontology collections of the Sorbonne Université (SU), formerly Université Pierre et Marie Curie, in Paris, also holds part of the Alexandre BRONGNIART's collection (BRIGNON, 2017). Since my 2014 publication (BRIGNON, 2014), I have rediscovered in SU an additional Muse specimen from the BRONGNIART collection (Fig. 1.A-B). It is labelled "*Palaeothrissum inaequilobum* BL. [BLAINVILLE]" and is the counterpart of the second specimen depicted in the drawing (Fig. 1.E, above). The SU specimen is therefore one of the syntypes of *Palaeothrissum inaequilobum* BLAINVILLE, 1818. A second specimen labelled "*Palaeothrissum inaequilobum* BL. [BLAINVILLE] de Muse" from the BRONGNIART collection is also kept in SU (SU.PAL.2017.0.1.17, former number 12887). The label indicates "Renaud ST AMOUR, 1833". The specimen was thus discovered or given to BRONGNIART in 1833 and therefore is not a syntype of *P. inaequilobum*. Anne-Nicolas-Joseph Renaud SAINT-AMOUR (1778-1869) was born in Saint-Amour (Jura). After his retirement from the military in 1830, he devoted himself to geological research and mine exploitation (DUFAY, 1874, p. 427).

BLAINVILLE (1818a, p. 321; 1818b, p. 17) distinguished the species *P. inaequilobum* and *P. parvum* on the observation that the two "lobes" of the caudal fin are almost equal in length in *P. parvum* whereas the upper "lobe" of *P. inaequilobum* is longer than the lower one. He also noted that *P. parvum* was slightly more elongated than *P. inaequilobum*. These distinctions are evident in the identified syntypes of both species (Fig. 1) but are, in fact, due to taphonomic distortions. Therefore the two species are synonyms, thus confirming the conclusion of previous authors (AGASSIZ, 1833; SAUVAGE, 1890; WOODWARD, 1891). The morphology of both specimens is typical of other specimens commonly assigned to *Aeduella blainvillei* (AGASSIZ, 1833) (HEYLER, 1969).

4. Nomenclatural status of *Aeduella blainvillei* (AGASSIZ, 1833)

As outlined above, *Palaeoniscum blainvillei* AGASSIZ, 1833, is an objective junior synonym of "*Palaeothrissum inaequilobum* BLAINVILLE, 1818, and "*Palaeothrissum parvum* BLAINVILLE, 1818. However, replacing the specific name *Aeduella blainvillei* (AGASSIZ, 1833) with *Aeduella inaequiroba* (BLAINVILLE, 1818) or *A. parva* (BLAINVILLE, 1818) is not in the interest of nomenclatural stability. To mediate the Principle of Priority, Article 23.9.1 of the International Code of Zoological Nomenclature (ICZN, 1999) allows for a reversal of precedence of a junior synonym when the senior synonym has not been used as a valid name after 1899 (Article 23.9.1.1) and the junior synonym "has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years" (Article 23.9.1.2).

To the best of my knowledge, the species names "*Palaeothrissum inaequilobum* BLAINVILLE, 1818, and "*Palaeothrissum parvum* BLAINVILLE, 1818, were not used as valid since 1899 thus fulfilling article 23.9.1.1 of the Code. Clearly giving priority to *Aeduella blainvillei* (AGASSIZ, 1833), WESTOLL (1937, p. 554) and HEYLER (1969, p. 98; 2000, p. 34-35) mentioned *Palaeothrissum inaequilobum* and *P. parvum* but did not consider them as valid. In BRIGNON (2014), these species were mentioned as well but were not considered as valid since their syntypes were clearly assigned to *Aeduella blainvillei* (AGASSIZ, 1833) (BRIGNON, 2014, Fig. 4). Furthermore, *Aeduella blainvillei* has been used as a valid name in at least 25 publications (see Appendix), published by at least 10 authors during the past 50 years and encompassing a span of not less than 10 years (condition 23.9.1.2). Thus *Aeduella blainvillei* (AGASSIZ, 1833) is regarded as valid, qualifying as a *nomen protectum*, whereas *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *Palaeothrissum parvum* BLAINVILLE, 1818, are recognized as invalid, qualifying as *nomina oblita*.

In his original description of *Palaeoniscum blainvillei*, AGASSIZ (1833) referred to many specimens without any clear indication of a type. According to article 72.1.1 of the International Code of Zoological Nomenclature, all these specimens belong to the type series. These include specimens in the collections of the Museum of Strasbourg and in the cabinets of natural history of Lausanne and Neuchâtel. He also referred to specimens in the collections of Alexandre BRONGNIART and François Théophile Marie RÉGLEY (1777-1833) who inherited the collection of FAUJAS de SAINT-FOND (BRIGNON, 2015a). Syntypes of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *P. parvum* BLAINVILLE, 1818, are therefore also part of the type series of *Palaeoniscum blainvillei*. As AGASSIZ wrote, the Muséum d'Histoire naturelle, Paris, possessed a wealth of specimens submitted by the geologist Augustin Henri de BONNARD (1781-1857). Four of the specimens from the Museum of Strasbourg are of particular interest since they were figured by AGASSIZ (1833, vol. 2, Pl. 5, figs. 1-4). Three of them are still held in the palaeontology collections of the Université de Strasbourg (UNISTA) (HEYLER, 1969, p. 132-133; 2000, p. 35). These specimens are numbered UNISTA.2013.0.133 (former numbers ST1 and AUT161), UNISTA.2013.0.135 (former numbers ST3 and AUT163), and UNISTA.2013.0.136 (former numbers ST4 and AUT164), corresponding, respectively, to the figures 2, 1 and 4 published by AGASSIZ (1833, vol. 2, Pl. 5) (Fig. 2). HEYLER (1969) designated specimen UNISTA.2013.0.133 (former numbers ST1 and AUT161) as the holotype of *Aeduella blainvillei*. This author, when wrongly using that term, explicitly indicated that he was selecting that particular specimen from the type series illustrated by



Figure 2: A, lectotype of *Aeduella blainvillei* (AGASSIZ, 1833) [*nomen protectum*] from Muse, "Autunian" continental stratotype (= Asselian), UNISTA.2013.0.133. B, figure of the same published by AGASSIZ (1833, vol. 2, Pl. 5, fig. 2). C and E, paralectotypes of *Aeduella blainvillei* from Muse, "Autunian" continental stratotype (= Asselian); C, UNISTA.2013.0.136. D, figure of the same published by AGASSIZ (1833, vol. 2, Pl. 5, fig. 4). E, UNISTA.2013.0.135. F, figure of the same published by AGASSIZ (1833, vol. 2, Pl. 5, fig. 1). Scale bar: 30 mm.

AGASSIZ to serve as the name-bearing type. According to Article 74.5 of the Code, this act can be considered as a lectotype designation. All the other specimens mentioned by AGASSIZ in his original description therefore become paralectotypes in accordance with Article 74.1 of the Code. Known paralectotypes are UNISTA.2013.0.135 (AGASSIZ, 1833, vol. 2, Pl. 5, fig. 1) (Fig. 2.E),

UNISTA.2013.0.136 (AGASSIZ, 1833, vol. 2, Pl. 5, fig. 4) (Fig. 2.C), MNHN.F.AUT704 (BRONGNIART collection number 12886), MNHN.F.AUT676 (BRONGNIART collection number 12890), MNHN.F.AUT25 (BRONGNIART collection number 12888) (Fig. 1.C) and SU.PAL.2017.0.1.16 (BRONGNIART's collection number 12889) (Fig. 1.A).



5. Systematic palaeontology

Class Osteichthyes HUXLEY, 1880

Subclass Actinopterygii COPE, 1887

Order Aeduelliformes HEYLER, 1969

Family Aeduellidae ROMER, 1945

Genus *Aeduella* WESTOLL, 1937

Type species.- by monotypy: *Palaeoniscum blainvillei* AGASSIZ, 1833 (*nomen protectum*), junior synonym of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *Palaeothrissum parvum* BLAINVILLE, 1818 (*nomina oblita*).

Statigraphic and geographic distributions of the genus.- Upper Carboniferous (Pennsylvanian) and Lower Permian (Cisuralian) from France, the Czech Republic, Germany and Switzerland (POPLIN & DUTHEIL, 2005).

***Aeduella blainvillei* (AGASSIZ, 1833)**

Type material.- lectotype: UNISTA.2013.0.133 (Fig. 2.A); known paralectotypes: UNISTA.2013.0.135 (Fig. 2.E), UNISTA.2013.0.136 (Fig. 2.C), MNHN.F.AUT704 (BRONGNIART's collection number 12886) (BRIGNON, 2014, Fig. 4.A), MNHN.F.AUT676 (BRONGNIART's collection number 12890), MNHN.F.AUT25 (BRONGNIART's collection number 12888) (Fig. 1.C), SU.PAL.2017.0.1.16 (BRONGNIART's collection number 12889) (Fig. 1.A).

Type locality and horizon.- Muse (Saône-et-Loire), Schistes bitumineux (Muse formation), continental regional Autunian stratotype, Asselian stage.

Diagnosis.- see HEYLER (1969) and POPLIN & DUTHEIL (2005).

6. Conclusion

In conclusion, the type species by monotypy of the genus *Aeduella* WESTOLL, 1937 (Actinopterygii, Aeduelliformes, Aeduellidae), is *Palaeoniscum blainvillei* AGASSIZ, 1833 (*nomen protectum*), junior synonym of *Palaeothrissum inaequilobum* BLAINVILLE, 1818, and *Palaeothrissum parvum* BLAINVILLE, 1818 (*nomina oblita*). This nomenclatural act promotes stability and retains the widely used and accepted name *Aeduella blainvillei* (AGASSIZ, 1833) as a valid one.

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Appendix

A list of 30 publications by 33 different authors published in the last 50 years, using *Aeduella blainvillei* (AGASSIZ, 1833) as a valid name to fulfill the requirements of Article 23.9.1.2 of the International Code of Zoological Nomenclature (ICZN, 1999):

BLIECK *et al.*, 1999; BOY & SCHINDLER, 2000, p. 124; BRIGNON, 2014, 2015b; BÜRGIN, 1990; DIETZE, 1999, 2000; GAND *et al.*, 2017; GOTTFRIED, 1987; HEYLER, 1969, 1991, 2000; HEYLER & PACAUD, 1978; HEYLER & POPLIN, 1983, 1988, 1990; MARTEAU, 1983, p. 61; PELLENARD *et al.*, 2017; POPLIN, 2001; POPLIN & DUTHEIL, 2005; RAT, 1972, p. 152; SCHINDLER, 2003; ŠTAMBERG, 1981, 2006, 2010, 2013a, 2013b, 2016a, 2016b; STEYER *et al.*, 2000.