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REDESCRIPTION OF '*PERLEIDUS*' (OSTEICHTHYES, ACTINOPTERYGII) FROM THE EARLY TRIASSIC OF NORTHWESTERN MADAGASCAR

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Abstract. The revision of the material from the Lower Triassic fossil-bearing-nodule levels from northwestern Madagascar supports the assumption that the genus *Perleidus* De Alessandri, 1910 is not present in the Early Triassic. In the past, the presence of this genus has been reported in the Early Triassic of Angola, Canada, China, Greenland, Madagascar and Spitsbergen. More recently, it has been pointed out that these taxa may not be ascribed to *Perleidus* owing to several anatomical differences. The morphometric, meristic and morphological analyses revealed a remarkable ontogenetic and individual intraspecific variation among dozens of specimens from the lower Triassic of Ankitokazo basin, northwestern Madagascar and allowed to consider the two Malagasyan species *P. madagascariensis* Piveteau, 1934, and *P. piveteaui* Lehman, 1952, as a single one and to ascribe it to the new genus *Teffichthys*. This new genus exhibits a unique combination of features, mainly in the skull dermal bone pattern and structure of caudal fin, that clearly support its exclusion from Perleidiformes. We also suggest to extend the use of *Teffichthys* for the other Early Triassic '*Perleidus*' species except those from southern China.

INTRODUCTION

The marine Early Triassic localities from the Ankitokazo basin, Diégo Suarez Province, northwestern Madagascar, yielded a well-diversified ichthyofauna, mainly composed by actinopterygian and sarcopterygian fishes preserved as negative print into siliceous nodules (Beltan 1996). This assemblage has been extensively studied in the XX century by Piveteau (1929, 1930, 1934, 1940), Lehman (1948, 1952, 1956), Lehman et al. (1959), Beltan (1957, 1968, 1996) and, more recently, Kogan & Romano (2016). Starting from Piveteau (1935), several studies pointed out the similarity between the Early Triassic fish assemblage of Madagascar and those of other localities. In fact, most of the fish genera found in the Early Triassic Malagaysian deposits (e.g., *Australosomus, Birgeria, Bobasatrania, Boreosomus, Helmolepis*, *Pteronisculus, Saurichthys* and Parasemionotiformes other than '*Perleidus*') have an almost worldwide distribution and were commonly found in Spitsbergen (Stensiö 1921), Greenland (Stensiö 1932), Canada (Schaeffer & Mangus 1976; Neuman 1986, 2015), Angola (Teixeira 1947; Antunes et al. 1990), and China (Su 1981; Tong et al. 2006). Due to the great similarity in their taxonomic composition, these assemblages have been recently indicated as Triassic Early Fish Fauna (TEFF in Tintori et al. 2014).

Traditionally, the genus *Perleidus* has been regarded as one of the most common representatives of the TEFF and several species have been created from different Lower Triassic deposits, starting from *P. woodwardi* from Spitsbergen (Stensiö 1921), *P. stoschiensis* from Greenland (Stensiö 1932), *P. madagascariensis* and *P. piveteaui* from Madagascar (Piveteau 1934; Lehman 1952), *P. lutoensis* and *P. lehmani* from Angola (Antunes et al. 1990), and *P. yangtzensis* and related species from southern China (Su 1981). However, the genus *Perleidus* was established by De Alessandri in 1910 based on material from the Middle Triassic (Late Ladinian) of Perledo (Lecco, Italy) housed at Senckemberg Museum of Frankfurt. Discovery of several specimens in the

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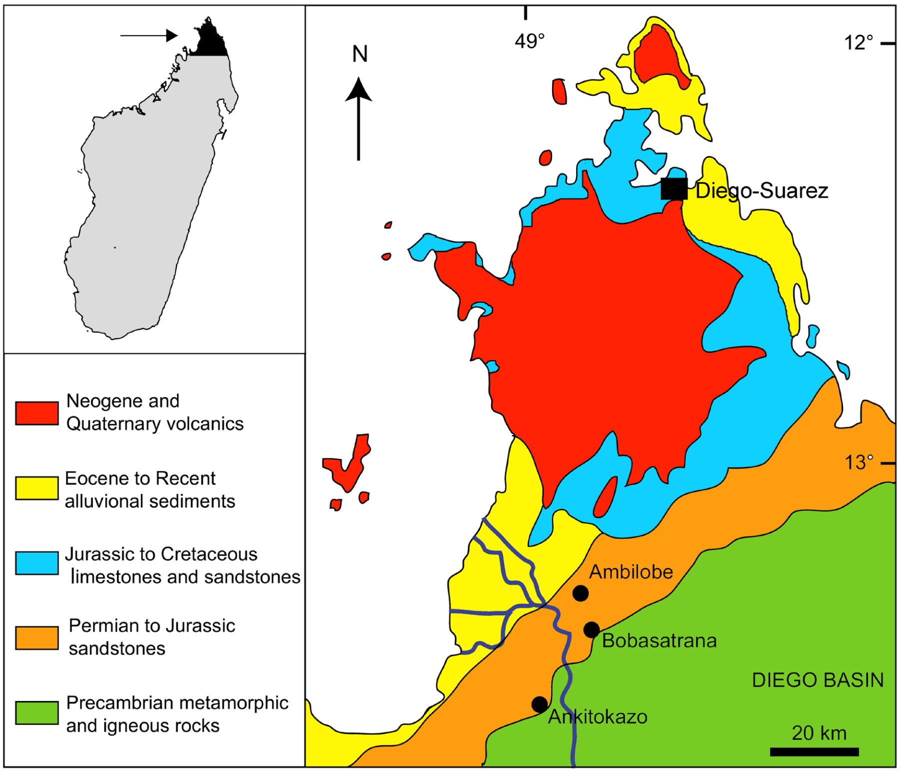


Fig. 1 - Location and simplified geological map of northwestern Madagascar showing the localities of Early Triassic age (full circles), where the *Teffichthys madagascariensis* remains have been collected. After Besairie (1968, 1969).

coeval strata of the Kalkschieferzone (uppermost Meride Limestone) from Ca' del Frate (Monte San Giorgio area, Viggiù, Varese, Italy) in the 1980/90s, allowed to properly define the diagnostic characters of the type species *Perleidus altolepis* (Deecke, 1889) and consequently the characteristics of the genus itself (Lombardo 1995, 2001; Lombardo et al. 2011). Lombardo (2001) therefore suggested that all *Perleidus* species from the Early Triassic of Greenland, Canada, Spitsbergen, Angola, Madagascar and China were incompatible with this genus, as all available complete specimens did not show epaxial rays in the caudal fin, but an abbreviate heterocercal tail, with a dorsal body lobe much shorter than in more basal 'paleopterygians' and thus similar to that of basal neopterygians.

In the present work, a large number of specimens from Ambilobe, Ankitokazo and Bobasastrana localities, in the Ankitokazo basin, northwestern Madagascar (Fig. 1), have been studied in order to verify the consistence of the genus '*Perleidus*' in the Malagasyan Early Triassic fish assemblage. Since the anatomical features confirm that the specimens cannot be attributed to the genus *Perleidus*, or to other known similar Triassic actinopterygian fishes, we therefore erect a new genus in order to contain all the material from the Early Triassic of Madagascar previously referred to *Perleidus*.

THE MADAGASCAR TRIASSIC EARLY FISH FAUNA (TEFF) ASSEMBLAGE

The new genus described herein, together with *Bobasatrania*, *Australosomus*, *Saurichthys*, 'paleonisciforms' and parasemionotiforms, is one of the most common early actinopterygian representatives in the TEFF assemblage from northwestern Madagascar (see Barbieri & Martin 1996; Beltan 1996; Tintori et al. 2014). However, it must be pointed out that material from Madagascar has been gathered from local people, who mostly collect it loose in the countryside and in the forest. Thus, any restoration regarding the Malagaysian Early Triassic faunal assemblages is spoiled by lack of stratigraphic and geographic data and also by collecting bias such as completeness and size of the fish bearing nodules, as well as by the fossil traders' choices. Nevertheless, the total assemblage from Madagascar is quite diversified and it is, as a whole, comparable to those from Greenland and Spitsbergen, even if most of the taxa are in need of systematic revision (see also Grande & Bemis 1998, for the parasemionotiform genera).

Concerning dating, fishes, temnospondylian amphibians, ammonites, conchostracans and shrimps from the Malagaysian TEFF have been described as a single assemblage from the Middle Sakaamena

Formation (Besaire 1972), but no detailed stratigraphical data are available. We must underline that this unit is very thick, from 300 to more than 600 m (Besaire 1972) but nobody has never given the fossiliferous horizon(s) detailed position. Beltan (1996) and Steyer (2002) recorded fishes and amphibians as from the Dienerian (Induan), while following Yanbin et al. (2002) the assemblage should be Smithian (early Olenekian) on the base of conchostracans. However, the use of fresh-water dwellers as guide-fossils over long distances, in this case *Euestheria (Magniestheria) truempyi* used to correlate the German Basin with the northwestern Madagascar, makes the correlation not sound at all, we tentatively date our specimens to Dienerian/Smithian, which is also the time when many others major Early Triassic fish beds formed around the Pangaea (Tintori et al. 2014).

Furthermore, it could also be possible that several different fish-bearing levels are present, since excavations on scientific bases have never been accomplished. As noted by Tintori et al. (2014), latest Permian-lower Triassic fish-beds around Pangaea can be related to global anoxic events, thus, as the Sakaamena formation is very thick, we can suppose the presence of several fossiliferous nodule horizons between the end Permian, as nodules with Permian ammonoids are known from the area (A.T. pers. obs.) and the end Smithian. Barbieri & Martin (1996) considered the material as belonging to separate assemblages, just on the basis of different collecting areas from the NW Madagascar. However, they did not explain if the recorded differences are to be considered as due to paleoenvironmental conditions inside the basin or to age shifting or both the settings. The geological succession of the Lower Triassic from which the fossil fishes considered in this study come from, are in the basin of Ankitokazo around Ambilobe (Province of Diego Suarez, northwestern Madagascar). Here, the fossils are collected mainly in nodules, as most of the published TEFF specimens from Greenland, Spitsbergen and China (Tintori et al. 2014). Nodules are found in laminated marly limestones/mudstone and elsewhere they are calcareous, with skeleton remains that can be more or less three-dimensional. However, the Malagaysian nodules are siliceous with some 11% of iron oxides, 5% of clay and titanium oxide and other trace minerals for 4% (Besairie 1972) although we still do not know their full diagenetic history. Most of the Madagascar specimens are just molds, as bones and scales have been diagenetically dissolved after the nodules have formed. As most of the specimens were well-preserved and almost perfectly articulated, starting of nodule formation must be considered as sinsedimentary. Bubbles possibly generated from gas decay are seldom preserved (A.T. pers. obs.), supporting the very early hardening of the sediment surrounding the specimen.

So far, no detailed studies have been done to ascertain if the modern nodule composition is the original one or if it is due to more or less late diagenetic processes that could have also influenced (dissolved) the bones and scales of fishes and amphibians. Besairie (1972) suggests that the very high ratio of iron oxide (11%) could indicate that the initial composition of the nodule was iron carbonate (such as the Carboniferous Mazon Creek nodules), who later suffered a replacement of carbonate by silica. Beltan (1996) suggests that it was the same initial sediment, made of silica, iron oxide and volcanic minerals coming from the nearby land, that hardened forming the nodule interacting with the acid product of the proteins. According to Beltan (1996) the decay process generated sulfuric acid that reacted with the phosphate of the bones and scales and the calcium carbonate of the ammonite shells to dissolve them in this early stage. However, this contrasts with the fact that the fossil impressions are very precise and detailed, indicating that at least mineralized structures break-down must have occurred well after the formation of the nodule and also that ammonoid aragonite shells and vertebrate bones show a very different taphonomic behavior. It is also possible that the dissolution of the skeletal remains is simply due to the heavy weathering in the tropical environment when the rocks reached close to the surface as in most nodules the tail of the fish is not totally enclosed in the nodule itself allowing the bones to be in contact with the surrounding environment. This could explain also the presence of iron oxides in the space left by the bone dissolution.

The Early Triassic northwestern Malagaysian localities yielded also a rich and well-diversified invertebrate (ammonoids, molluscs and crustaceans), but scarce terrestrial plant remains. Ammonites are stenohaline marine organisms while amphibians and conchostracans are fresh water dwellers even if sometimes they can enter brackish waters. Regarding fishes some of them are clearly stenohaline marine as they have been found only in surely marine environments in Greenland, China, Canada and Alps, pointing to a salted environment for the fish assemblage, even if close to the coast (Beltan 1996). So far, it was impossible to ascertain if temnospondylian amphibians, present also in the Early Triassic from Spitsbergen, are from interbedded fresh water levels, possibly yielding also the conchostracans, or entered the sea forestalling the Spathian blooming of the marine reptiles (Jiang et al. 2012). A detailed bed by bed collecting will be necessary to settle the paleoenvironmental interpretation, although the preservation in some of the nodules of fish and ammonoids together (A.T. pers. obs.) points to a marine environment at least for the depositional environment.

Material and methods

The present study is based on 45 fish specimens housed in the collections of the Museum National d'Histoire Naturelle in Paris (MNHN), Natural History Museum of London (NHM), Museo Civico di Storia Naturale di Milano, Italy (MSNM), and Museo di Paleontologia dell'Università di Milano (MPUM). All specimens were previously referred to the genus '*Perleidus*'. Since the dissolution of organic remains left only a negative print of the specimens, a silicone mold has been made to create a positive cast of some of the specimens. Casts and specimens were examined using different stereomicroscopes equipped with a camera lucida drawing arm. Measurements were taken using a dial caliper to the nearest 0.1 mm. Standard length (SL; measured from the tip of the snout to the base of the caudal fin across the lateral line) is used throughout. Osteological terminology adopted follows primarily the traditional actinopterygian nomenclature of Gardiner (1984) and Gardiner & Schaeffer (1989). The squamation formula used to describe the relative position of the fins on scale rows (insertion) follows Westoll (1944).

The quite large number of specimens, although they could be collected from different areas and fossiliferous horizons, allowed to test the homogeneity of the sample in order to confirm its assignment to a single species. All morphometric data were log-transformed and corrected for size using the standard length as the independent variable. Size-correction was not performed for meristic traits as they are independent of body size and are fixed during early ontogeny (Frey et al. 2016). Histograms illustrating the continuous variation of morphometric and meristic data are shown, and the least squares regression is used to obtain the relation between the standard length (SL) and other morphometric features. The relationships between the standard length and various morphometric features were analyzed for statistical outliers which deviate more than three standard deviations from the mean (see e.g., Simon et al. 2010). We also calculated the coefficient of variation (COV, calculated as standard deviation divided by the trait mean) for each character (using log-transformed and size-corrected data for morphometric parameters) in order to obtain an estimate of trait variability. Differences in variation between morphometric and meristic characters were tested using the Mann-Whitney U-test. Following Takács (2012), a principal component analysis (PCA) and the analysis of similarities (ANOSIM; Clarke 1993) were performed on the entire dataset of standardized morphometric and meristic parameters in order to establish the degree of interspecific variation by testing the differences between groups (species) defined a priori. Alpha was set at 0.05. The methods for the statistical analysis of data follow primarily Weitschat (2008), Marramà & Carnevale (2015) and Frey et al. (2016).

The geometric morphometric approach (Zelditch et al. 2004) was used in order to detect significant morphological variation, by analyzing the clustering of specimens on morphospace that could potentially represent different morphotypes or species. A total of nine homologous landmarks and 20 equidistant semilandmarks were digitized on photographs obtained from a subset of 34 well-preserved specimens using the software package TPSdig 2.05 (Rohlf 2005). The chosen landmarks and semilandmarks describe the shape of maxilla and the opercular series (including preopercle, opercle and subopercle), since the morphology and proportions of these bones were used by Lehman (1952) to distinguish the two Malagaysian species, and the opercular apparatus in particular is well-suited to geometric morphometric description (e.g., Kimmel et al. 2010; Wilson et al. 2013). After the landmark input, the shape variables were extracted by applying the Generalized Procrustes Analysis (GPA) through the software TPSrelw (Rohlf 2010). The GPA aligns the landmark configurations to a common reference (the consensus shape) after removing the effect of rotation, translation and size among specimens (Rohlf & Slice 1990). Moreover, the Partial Least Square analysis (PLS; Rohlf & Corti 2000) was applied to detect a possible ontogenetic relationship between shape and size. Detailed information about the generation of shape data and statistical analyses are provided in Marramà et al. (2016a, b, c).

Statistical analyses were performed through the software package PAST (Hammer et al. 2001). Supplementary material containing the data on which the analyses were performed is provided.

Anatomical abbreviations

AFB, anal-fin base; AFI, anal-fin insertion; AFR, anal-fin rays; ang, angular; ao, antorbital; bf, basal fulcra; br, branchiostegal rays; cl, cleithrum; CPD, caudal peduncle depth; CPL, caudal peduncle length; de, dentary; DFB, dorsal-fin base; DFI, dorsal-fin insertion; DFR, dorsal-fin rays; dpt, dermopterotic; ds, dermosphenotic; dy, dermohyal; ex, extrascapular; ff, fringing fulcra; fr, frontal; gu, gular; HD, head depth; HL, head length; HSR, horizontal scale rows; io, infraorbitals; ls, lateral line scales; MBD, maximum body depth; MSD, maximum scale depth; mx, maxilla; na, nasal; OD, orbit diameter; op, opercle; pa, parietal; PANA, preanal distance; PDOR, predorsal distance; PFI, pelvic-fin insertion; PFR, pectoral-fin rays; pmx, premaxilla; pop, preopercle; POSTO, postorbital length; PPEC, prepectoral distance; PPEL, prepelvic distance; PREO, preorbital length; ptt, posttemporal; PVFR, pelvic-fin rays; ro, rostral; SL, standard length; scl, supracleithrum; so, supraorbitals; sbo, suborbital; sop, subopercle; sp, spiracular; VSR, vertical scale rows;

SYSTEMATIC PALEONTOLOGY

Class **Osteichthyes** Huxley, 1880
Subclass **Actinopterygii** Woodward, 1891
incertae sedis
Genus *Teffichthys* gen. n.

Type species: *Teffichthys madagascariensis* (Piveteau, 1934)

Code Zoobank: urn:lsid:zoobank.org:act:55BF2EB3-B828-4C79-BFDD-C32144B9C082.

Origin of the name: Named after 'TEFF' (Triassic Early Fish Fauna; see Tintori et al. 2014), being one of the most common representatives of this assemblage, and from Greek 'ichthys', meaning 'fish'.

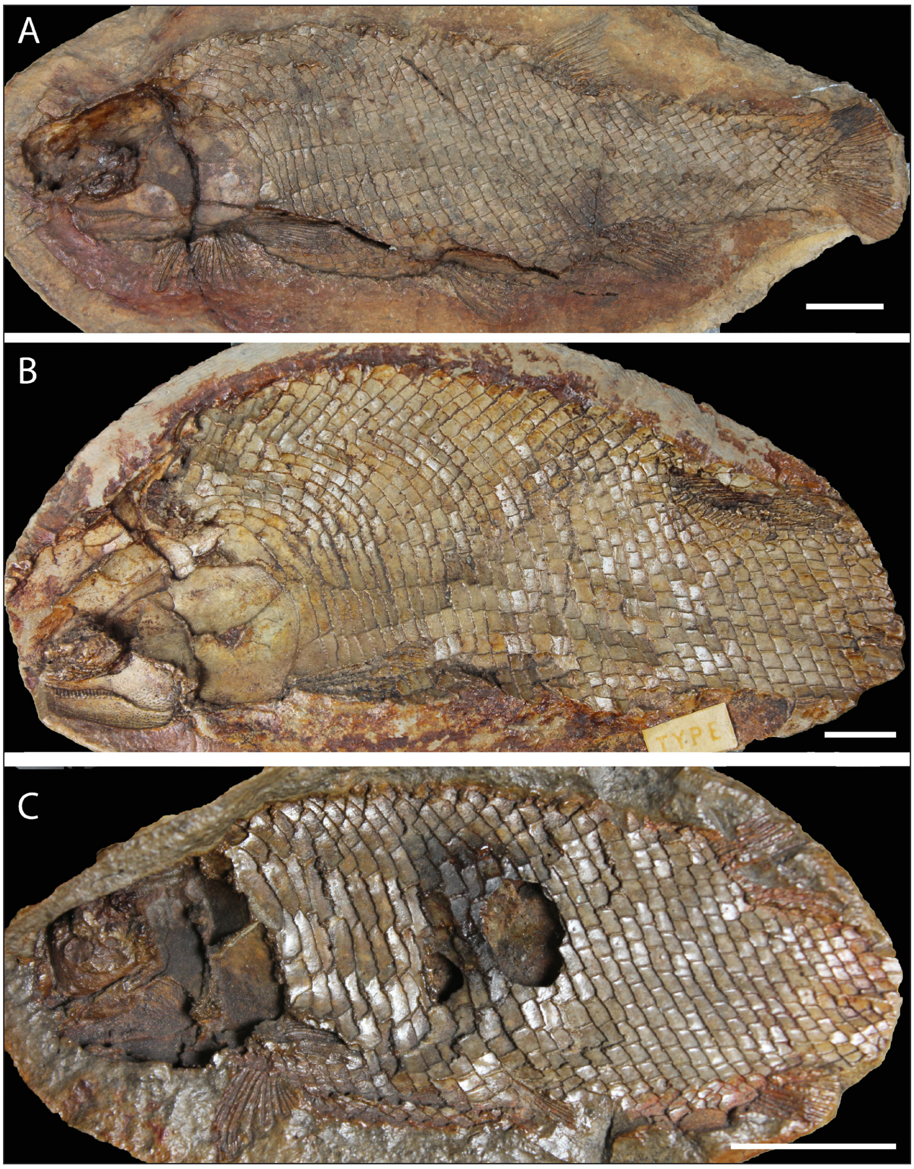


Fig. 2 - *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) from the Early Triassic of Madagascar; historical type series. A) MNHN F.MAE112, lectotype. B) MNHN F.MAE111, paralectotype. C) MNHN F.MAE113, paralectotype. Scale bars 10 mm.

Diagnosis: Small- to medium-sized basal (non neopterygian) actinopterygian fish having the following unique combination of characters: body elongate and tapered; dermal cranial bones ornamented with tubercles and ridges; parietals subquadrangular in shape with three pit-lines (anterior, median and posterior); posttemporals widely separated; suborbital and spiracular ossicles present; two to five supraorbitals; nasals separated by the rostral; maxilla fixed to an almost vertical preopercle; straight oral margin of maxilla, which is dorso-posteriorly expanded; jaws with styliform teeth; broad vertical or slightly forward inclined preopercle; opercle smaller than subopercle; five to eight branchiostegal rays; dorsal and anal fins inserted in the posterior half of the body; median-fin rays only distally segmented and supported by an equal number of pterygiophores at least in the middle part; fringing fulcra present on all fins; abbreviated heterocercal caudal fin; anteriormost lateral trunk scales higher than wide, with serrated posterior margin.

Remarks. The species *Perleidus madagascariensis* was erected by Piveteau (1934) who provided the description and figures based on a type series of three specimens (MNHN F.MAE111, 112, 113) coming from the Ankitokazo basin of northwestern Madagascar (the exact type locality is impossible to establish) and today housed on Museum National d'Histoire Naturelle of Paris (Fig. 2A-C). Following the erroneous interpretation of Stensiö (1921, 1932), who erected the species *Perleidus woodwardi* based on material from the Early Triassic of Spitsbergen, not fully considering the descriptions of Deecke (1889) and De Alessandri (1910), Piveteau (1934) attributed the material form Madagascar to the genus *Perleidus* De Alessandri, 1910. The attribution of the Malagaysian specimens to this genus has been justified primarily by comparison of the skull dermal bone and squamation patterns with the species from Spitsbergen rather than with the type species from Perledo. Subsequently, following Piveteau, Lehman (1952) erected a second species of *Perleidus* from the Early Triassic of Madagascar (*P. piveteaui*) based on a

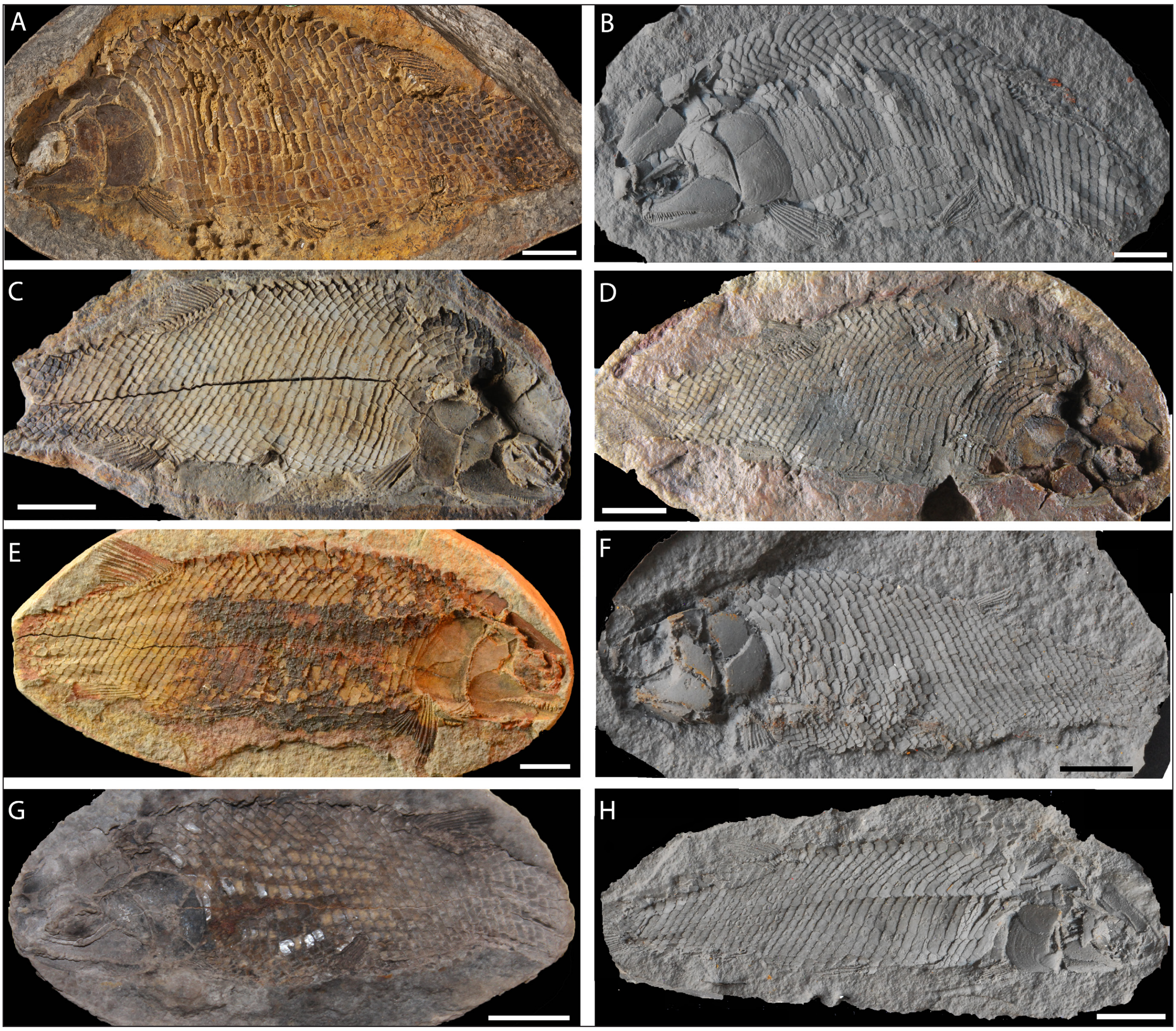


Fig. 3 - *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) from the Early Triassic of Madagascar. A) NHM P.19591, holotype of *'Perleidus' piveteaui*. B) MSNM V1723, silicon mold. C) MNHN F.MAE364. D) MNHN F.MAE125. E) MSNM V1845. F) MSNM V1862, silicon mold. G) MPUM 11585. H) MSNM V1356, silicon mold. Scale bars 10 mm.

few specimens housed on Natural History Museum of London (holotype NHM P.19591; Fig. 3A), providing a diagnosis for both species. According to Lehman (1952) *P. madagascariensis* and *P. piveteaui* differ from each other in the shape, morphology and proportions of some cranial bones, primarily the maxilla and opercular series; however, our revision of dozens of specimens recognized a continuous normal distributions in the morphometric, meristic and morphological characters that do not allow for a separation of the sample into different discrete groups (see Results and Discussion). The attribution of the Malagaysian species to the genus *Perleidus*, as well as the presence of this genus in the Early Triassic of several others sites, has been questioned for the first time by Lombardo (2001) who clearly defined the diagnostic characters of the type species *Perleidus altolepis* (Deecke, 1889) as well as the characters of the genus by analyzing several specimens from the upper Ladinian (Middle Triassic) levels of the Kalkschieferzone (Meride Limestone) of Ca' del Frate (Varese, Italy). As pointed out by Lombardo (1995, 2001), *Perleidus* is a fusiform small- to medium-sized fish showing basal non-neopterygian characters, typical of 'subholosteans', such as a large shield-like rostral, upper jaw with deep posterior region contacting the preopercle and lack of an interopercle, together with more derived characters in the postcranial skeleton. Among these, fin rays only distally segmented and supported by an almost equal number of endoskeletal elements, and an externally almost symmetrical hemiheterocercal caudal fin due to the presence of a variable number of epaxial rays (Lombardo 2001), a character representing a synapomorphy for the 'subholosteans' as stated originally by Gardiner (1988) and Gardiner & Schaeffer (1989). Despite the characteristics of rays and supports are traditionally considered typical of neopterygian fishes (Patterson 1973; but see also Tintori et al. 2008, 2012; Sun et al. 2012), the caudal-fin pattern, which is always present in Perleidiformes and Peltopleuriformes, is not shared by neopterygians that show an abbreviated heterocercal tail in the basal forms and then a homocercal one in the teleosts. Since all available complete Early Triassic "*Perleidus*" specimens did not show epaxial rays in the caudal fin, but an abbreviate heterocercal tail, with a dorsal body lobe much shorter than in more basal 'paleopterygians' and thus similar to that of basal neopterygians, Lombardo (2001) suggested that *P. madagascariensis* and *P. piveteaui*, as well as the other '*Perleidus*' species from the Early Triassic of Spitsbergen, Greenland, Angola, and Canada, could not be assigned to *Perleidus*, whose only valid species is therefore *P. altolepis* from Late Ladinian of Perledo, Ca' del Frate (Italy) and Meride (Switzerland), to which was then added *P. sinensis* from Anisian of Luoping, South China (Lombardo 2001; Lombardo et al. 2011). Following Lombardo conclusions, Jin et al. (2003) suggested that the two Malagaysian species could then be referred to the Chinese genus *Plesioperleidus*, established by Su & Li (1983) on a single specimen from Olenekian (Early Triassic) of southern China. Unfortunately, the holotype and only specimen was apparently lost (confirmed by Jiang D.-Y., PKU, pers. comm. 2013, after new researches). As the original description of *Plesioperleidus* is not very informative, especially about the tail structure, Jin et al. (2003) ascribed the Chinese '*Perleidus*' species to *Zhangina* Liu et al., 2002. However, Tong et al. (2006), considering *Zhangina* as junior synonym of *Plesioperleidus,* moved the Chinese and Malagaysian species to this genus, also making a reduction of the species number considering some of them just as junior synonyms of previously described ones. The analysis of Jin et al. (2003) is incomplete, lacking of a comprehensive revision of the Malagaysian material, which consequently prevented the recognition of the real differences between *Plesioperleidus* (and/or *Zhangina*) and the species from Madagascar. *Plesioperleidus* differs from Madagascar '*Perleidus*' by having the supraorbital sensory canal traversing the entire length of parietal, pit-lines of parietal absent; no suborbital or spiracular ossicles; fewer than four supraorbital bones; three to four branchiostegals; dorsal ridgescales developed and spinous. In our opinion, the diagnosis of the genus *Plesioperleidus* (although based on incomplete specimens, lacking of caudal fin) by Tong et al. (2006) must be considered valid exclusively for the Chinese material. Therefore, we suggest that that the Malagaysian specimens documented herein cannot be attributed to *Plesioperleidus*. Thus, we erected *Teffichthys* as genus name to include at least the Madagascar '*Perleidus*' species.

Teffichthys madagascariensis comb. n.
(Piveteau, 1934)
Figs 2-13

1934 *Perleidus madagascariensis* Piveteau, p.43, pl.16, fig. 1-5.
1947 *Perleidus madagascariensis* - Teixeira, p. 105.
1952 *Perleidus madagascariensis* - Lehman, p.135, pl.27, fig. C.
1952 *Perleidus piveteaui* Lehman, p.141, pl.27, fig. B.
1955 *Perleidus madagascariensis* - Schaeffer, p. 4, figs. 6-7.
1981 *Perleidus madagascariensis* - Su, p. 110.
1981 *Perleidus piveteaui* - Su, p. 109.
1983 *Perleidus madagascariensis* - Su & Li, p. 14.
1989 *Perleidus madagascariensis* - Gardiner & Schaeffer, p. 179, fig. 6.
1990 *Perleidus madagascariensis* - Antunes et al., p. 24.
1990 *Perleidus piveteaui* -Antunes et al., p. 25.
1995 *Perleidus madagascariensis* - Bürgin, p. 806.
1995 *Perleidus madagascariensis* - Lombardo, p. 212.
1995 *Perleidus piveteaui* - Bürgin, p. 812.
1995 *Perleidus piveteaui* - Lombardo, p. 212.
1997 *Perleidus madagascariensis* - Qian et al., p. 67.
1997 *Perleidus piveteaui* - Qian et al., p. 67.
2001 *Perleidus madagascariensis* - Lombardo, p. 357.
2001 *Perleidus piveteaui* - Lombardo, p. 357.
2002 *Perleidus* aff . *P. madagascariensis* - Liu et al., p. 27.
2002 *Perleidus piveteaui* - Liu et al., p. 27.
2003 *Perleidus* aff. *P. madagascariensis* - Jin et al., p. 169.
2003 *Perleidus piveteaui* - Jin et al., p. 169.
2005 *Perleidus piveteaui* - Neuman & Mutter, p. 29
2006 *Perleidus* aff. *P. madagascariensis* - Tong et al., p. 148.
2006 *Perleidus piveteaui* - Tong et al., p. 148.
2011 *Perleidus* cf. *madagascariensis* - Lombardo et al., p. 78.
2011 *Perleidus piveteaui* - Lombardo et al., p. 78.
2015 *Perleidus madagascariensis* - Xu et al., p. 2, fig. 9.

Lectotype*:* MNHN F.MAE112, nearly complete articulated specimen on a hemi-nodule (Fig. 2A), 94.3 mm SL; Early Triassic (Dinerian/Smithian), Ankitokazo Basin, Madagascar. It was chosen as lectotype among the specimens of the type series figured by Piveteau (1934) because it shows most of the characters useful to redefine the genus.

Paralectotypes*:* MNHN F.MAE111, an almost complete articulated specimen on a hemi-nodule (Fig. 2B), 129.3 mm SL; MNHN F.MAE113, nearly complete articulated specimen on a hemi-nodule, 72.1 mm SL. (Fig. 2C).

Referred material: Additional 42 specimens: MNHN F.MAE1023; MNHN F.MAE361; MNHN F.MAE652; MNHN F.MAE1111; MNHN F.MAE125; MNHN F.MAE1282; MNHN F.MAE1283; MNHN F.MAE1284; MNHN F.MAE1371; MNHN F.MAE364; MNHN F.MAE365; MNHN F.MAE366; MNHN F. MAE371; MNHN F.MAE378; MNHN F.MAE379; MNHN F.MAE51; MNHN F.MAE526; MNHN F.MAE646; MNHN F.MAE847; MPUM 11585; MPUM 11586; MSNM V1266; MSNM V1356; MSNM V1369; MSNM V1705; MSNM V1708; MSNM V1723; MSNM V1730; MSNM V1765; MSNM V1769; MSNM V1777; MSNM V1782; MSNM V1845; MSNM V1862; MSNM V1925; MSNM V1945; MSNM V3191; MSNM V7116; MSNM V7117; MSNM V7118; NHM 19580; NHM 19591-2.

Type locality: Ankitokazo basin (Diego Suarez Province, Ambilobe region), northwestern Madagascar; Early Triassic (Dienerian/Smithian).

Diagnosis: Medium sized *Teffichthys* (the largest specimen measuring about 129 mm SL) having head length and body depth contained about 3.5 in the SL; single suborbital; single spiracular; four supraorbitals; five to six branchiostegal rays; about 40 vertical and 13 horizontal scale rows; dorsal-ridge scales heart-shaped, not spinous; predorsal distance about 71% SL; prepelvic distance about 57% SL; preanal distance about 76% SL; squamation formula D25/P13 A21 C37/T40.

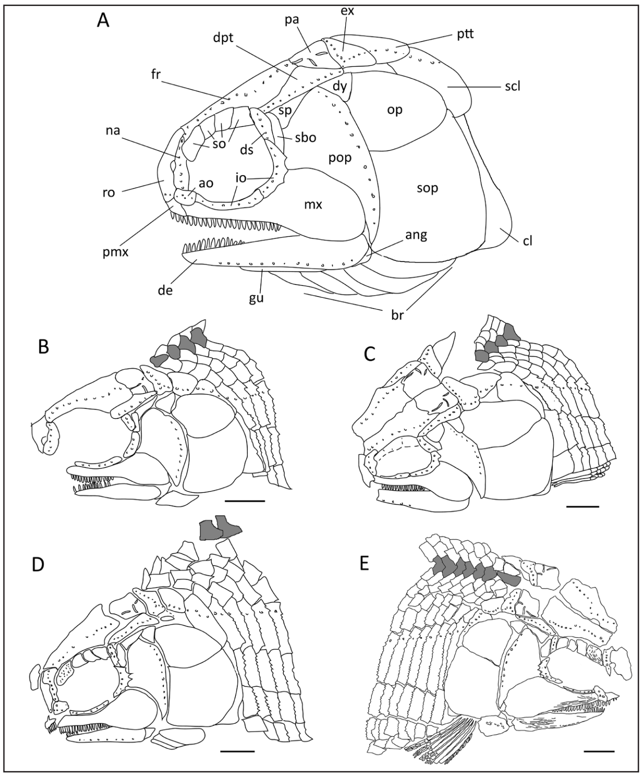
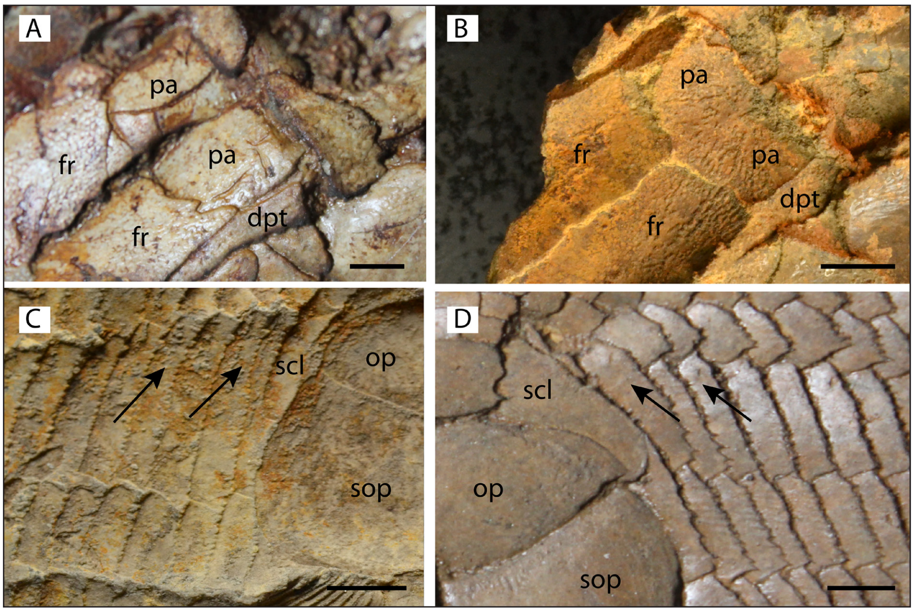


Fig. 4 - *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) from the Early Triassic of Madagascar. A) Reconstruction of the head and pectoral girdle. B) MNHN F.MAE112, lectotype. C) MNHN F.MAE111, paralectotype. D) NHM P.19591, holotype of *'Perleidus' piveteaui*. E) MSNM V1723. Scale bars 5 mm. The mid-dorsal ridge scales are in grey.

Description. Counts and measurements for *Teffichthys madagascariensis* are given in Tables 1 and 2. The observed specimens range between 51 and 129 mm SL. The body is fusiform and the head is large, its length contained about 3.5 in the SL. The snout is blunt and the mouth terminal and large. The maximum body depth is contained about 3.5 times in the SL. The body is entirely covered with ganoid scales. The dorsal and anal fins are located in the posterior half of body. All the fins contain distally segmented rays and bear fringing fulcra. The caudal fin is forked and abbreviated heterocercal.

Dermatocranium. The description of the cranial structures (Fig. 4A-E) is based primarily on the specimens MNHN F.MAE111, MNHN F.MAE112, MSNM V1723 and NHM P.19591 (Figs 2A-B, 3A-B). The rostral [= postrostral of Piveteau (1934) and Lehman (1952)] is the largest bone of the snout region, being about half of the length of the frontal, with which is in contact posteriorly; the rostral is subrectangular, shield-like, and reaches its largest width dorsally. Two notches for the nostrils lie at about mid-level of its lateral margins. The absence of teeth on the rostral may indicate that this bone does not contribute to the upper oral margin. The rostral separates completely the two nasal bones; they are narrowed and dorso-ventrally elongated, slightly shorter than the rostral; the median margin of the nasals bears a small notch for the anterior nostril. The sensory canal crosses dorso-ventrally the length of the nasals reaching the frontal dorsally and the antorbitals ventrally. The frontals are broad and subtrapezoidal in shape with an expanded postorbital region; these are the largest bones of the skull roof, occupying about 60-70% of the total cranial length. The posterior margin of the frontal is straight or slightly wavy, although in a single case (MNHN F.MAE111; Fig. 4C, 5A) it bears a small lateral indentation inserting between the parietal and dermopterotic that was interpreted as an intertemporal ossicle by Lehman (1952). The interfrontal suture is mostly straight although in few specimens a zigzag suture characterizes the median margin of the frontals. From the nasal, the supraorbital sensory canal enters at the antero-lateral corner of the frontal, reaching the posterior margin of the bone and ending on the anterior pit-line of the parietals. The parietals are small, quadrangular in shape, and bear three distinct pit-lines on anterior, lateral and posterior margin of each bone, respectively. The interparietal suture is straight, as well as the articulation with the frontals anteriorly, the dermopterotic laterally, and the extrascapular posteriorly. In a single

Fig. 5 - Individual variation in *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) from the Early Triassic of Madagascar. A) MNHN F.MAE111, specimen showing the frontal with a small lateral indentation inserting between the parietal and dermopterotic. B) MSNM V3191, specimen with parietals fused into a single shield. C) MSNM V1723, anteriormost lateral scales. D) MNHN F.MAE51, anteriormost lateral scales. The arrows indicate the scales supporting the lateral line. Scale bars 2 mm.



specimen (MSNM V3191; Fig. 5B) the parietals are completely fused into a single subrectangular shield; this condition can be interpreted as a case of individual variation (see Discussion). The dermopterotic is narrow, subtriangular in shape, antero-posteriorly elongated and articulating dorsally with the posterior region of the frontal and parietal for its entire length; the dermopterotics are crossed longitudinally by the supratemporal sensory canal that posteriorly enters the extrascapulars. The extrascapulars are subtriangular in shape; their anterior margin contacts the parietal and the dermopterotic, whereas posteriorly they articulate with the posttemporal; the extrascapulars join each other medially transmitting the supratemporal commissural canal. All the bones of the skull roof are ornamented with tubercles or ridges. The ornamentation is stronger in large individuals, whereas it is weak or completely absent in the smallest specimens. *Teffichthys* gen. n. is characterized by the presence of a single spiracular ossicle, triangular in shape, lying between the preopercle, suborbital and dermopterotic. This single bone is clearly visible in most of the specimens, including the lectotype (MNHN F.MAE112; Figs 2A, 4B) and paralectotypes (e.g., MNHN F.MAE111; Figs 2B, 4C). A small subtriangular dermohyal inserts between the opercle, preopercle and dermopterotic.

Circumorbital series. The dorsal margin of the orbit is bordered by four large quadrangular supraorbitals supported by the anterior margin of the frontal. The anteriormost supraorbital is the largest of the series and is ornamented with ridges or tubercles. The antorbital [= rostral of Piveteau (1934) and Lehman (1952)] is small and irregular in shape; it articulates with the rostral and nasal antero-dorsally, the premaxilla ventrally and the first infraorbital posteriorly. Both the ethmoid and the infraorbital sensory canals meet on the antorbital. Two infraorbitals surround the ventral margin of the orbit; the anteriormost element is thin, antero-posteriorly elongated and slightly bent, whereas the other one is crescent-shaped and boards the postero-ventral margin of the orbit; the second infraorbital bears more or less developed spines along its posterior margin. The dermosphenotic is thin, dorso-ventrally elongated and forms the postero-dorsal margin of the orbit. The infraorbital sensory canal crosses the entire length of the infraorbitals and dermosphenotic, entering the dermopterotic. There is a single suborbital lying posteriorly to the dermosphenotic, and almost of equal in size and shape. The posterior margin of the suborbital is smooth, not serrated (as in *Perleidus altolepis*).

Jaws. The premaxilla is small and bears four or five teeth similar in shape and size to those of the maxilla. The maxilla is large, antero-posteriorly elongated and posteriorly expanded; the oral margin is straight and bears a row of about 20 slender, styliform teeth, decreasing in size posteriorly. The maxilla is strongly ornamented of small tubercles or ridges. The dentary is slender, antero-posteriorly elongated; its oral margin is straight and bears a row of styliform teeth, less numerous than those of the maxilla; the outer ornamentation is made of ridges and tubercles running antero-posteriorly. The man-

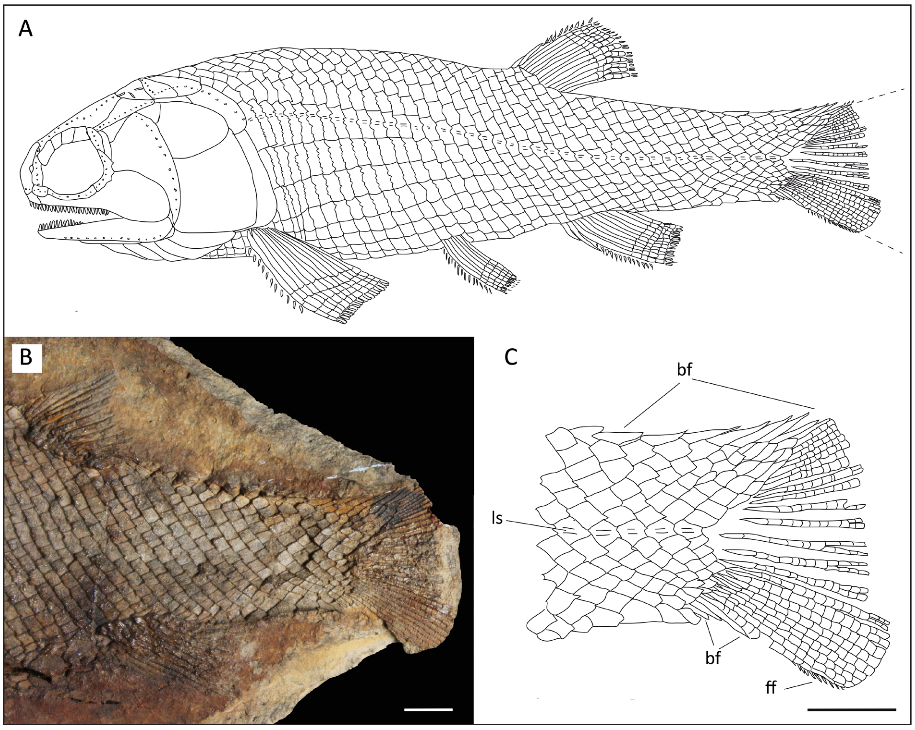


Fig. 6 - A) Reconstruction of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) primarily based on lectotype and paralectotypes. B) MNHN F.MAE112, lectotype, close-up of the caudal fin and the posterior half of the body. C) Drawing of the caudal fin of MNHN F.MAE112. Scale bars 5 mm.

dibular sensory canal crosses antero-posteriorly the entire length of the dentary. The dentary is posteriorly bounded by a small angular.

Operculo-gular series. The preopercle is broad, vertical or slightly inclined forward, and subquadrangular in shape; its antero-ventral margin embraces the postero-dorsal margin of the maxilla through a straight to curve suture; the preopercular sensory canal crosses dorso-ventrally this bone along its posterior border. The opercle is quadrangular in shape, as deep as wide with rounded margins; it articulates ventrally with the subopercle, through a gently curved margin. The subopercle is subrectangular in shape; its postero-ventral border is rounded, as well as its anterior margin; the subopercle is about 1.5-2 times larger than the opercle. There are five or six subrectangular branchiostegal rays, surrounding each side of the single ovoid gular. Due to taphonomic processes, the posteriormost branchiostegal often lies near the ventral margin of the subopercle, resambling an interopercle; however *Teffichthys* gen. n. lacks this bone.

Pectoral girdle. The posttemporals are subtriangular in shape and widely separated from each other by the mid-dorsal ridge scales; they contact anteriorly the extrascapulars from which they receive the sensory canal. The supracleithrum is deep, dorso-ventrally elongated, with a rounded posterior margin; it is often partially covered by the opercle. From posttemporal, the sensory canal enters at the antero-dorsal corner of the supracleithrum, reaching the posterior margin of the bone and ending in the deepest scale of the first scale row. The cleithrum is the largest bone of the pectoral girdle; it is deep, L-shaped and with the dorsal arm slightly more developed than the ventral one. There are no postcleithra.

Fins. Each pectoral fin is formed by 12 or 13, distally segmented bifurcated or multifurcated rays; several fringing-fulcra cover the anterior margin of the first ray (Figs 4E, 6A). The pelvic fins originate at the level of the 12-13th vertical scale row and contain 7-8 rays distally segmented; fringing-fulcra cover the entire length of first pelvic-fin ray. The median fins are posteriorly displaced behind the mid-length of the body (Fig. 6); two or three basal fulcra lie anteriorly to each median fin, and a large number of fringing-fulcra cover the first ray of both the dorsal and anal fins. The dorsal fin is nearly subtriangular in shape and inserts at the level of the 25th vertical scale row; it contains 14-15 distally segmented rays with the length of their proximal unsegmented portion measuring about 1/2 of the entire fin. The anal fin is slightly smaller than the dorsal one and it originates posteriorly to the 21st scale row; the anal fin contains about 11-12 distally segmented rays. The rays of both median fins are supported by an equal number of pterygiophores.

The caudal fin is forked and clearly abbreviate heterocercal, without epaxial rays (Fig. 6B-C); it contains about 20 proximally segmented rays and each lobe shows numerous fringing-fulcra. Seven to eight basal fulcra cover the dorsal lobe, and three to four the ventral one.

Squamation. The body is entirely covered by ganoid scales. Only the base of the dorsal and anal fins lacks one or two horizontal scale rows in the smallest individuals. The squamation consists of about 40 vertical and 13 horizontal scale rows. The dorsal-ridge scales are moderately developed, heart-shaped and not spinous (Fig. 4B-E). The lateral line scales, as well as those immediately above and below, are higher than long, becoming gradually smaller in the posterior region of trunk, where they assume a rhomboidal shape on the caudal peduncle. The depth of the anteriormost lateral line scale ranges from 1.1 (most commonly) to 2.5 times (rarely) that of the scale immediately below (Figs 4B-E, 5C-D). The outer surface of the scales is smooth and the posterior margin of the anteriormost flank scales shows numerous well-developed denticles, whose number decreases gradually posteriorly, in both the dorsal and ventral regions of the body. The serration of the scales is stronger and more evident in large specimens, whereas it is weak or totally absent in small individuals. The lateral line crosses throughout the length of the fish in the highest deepened flank scales.

BIOMETRIC ANALYSIS

The examination of the numerous specimens from Ankitokazo basin allowed us to test the homogeneity of the sample and, as a consequence, to confirm its assignment to a single taxon. The Table 3 shows the measurements and counts used to identify the specific biometric parameters of *Teffichthys madagascariensis* comb. n. The analysis of morphometric and meristic features shows that it is impossible to separate the sample into discrete groups. Histograms based on meristic count and size-frequencies (Figs 7 and 8) are normally distributed with a clear domination of intermediate forms and with comparably rare extremes. The regression lines of the morphometric characters analyzed (Fig. 9) show a high coefficient of determination ranging from

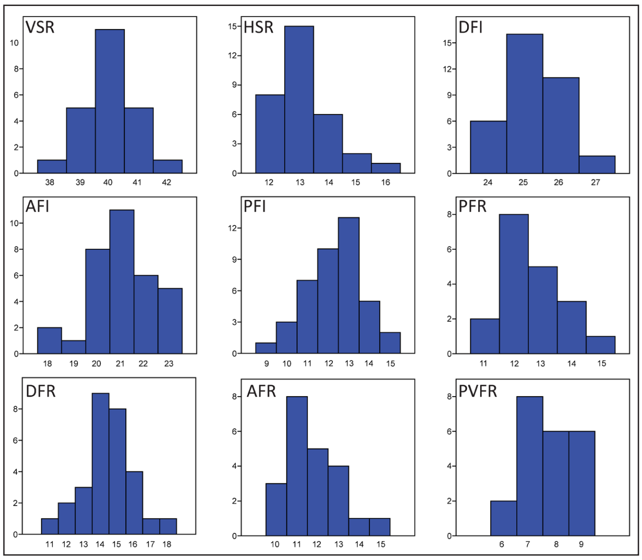


Fig. 7 - Histograms showing the distributions of meristic characters of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934). The x-axis represents the number of elements and the y-axis the relative frequency.

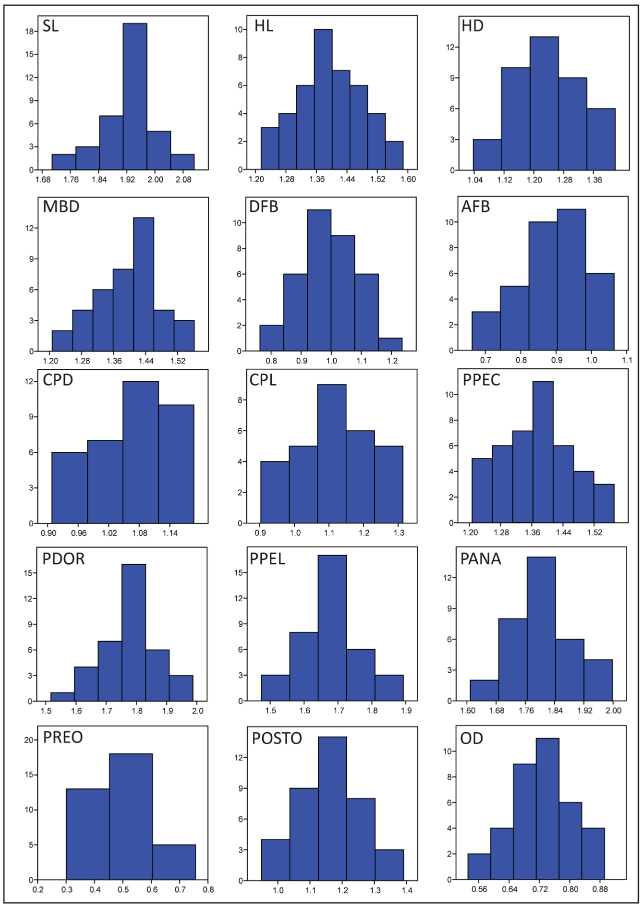


Fig. 8 - Histograms showing the size-frequency distributions for each morphometric character of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934). All the measurements are log-transformed and the y-axis represents the relative frequency.

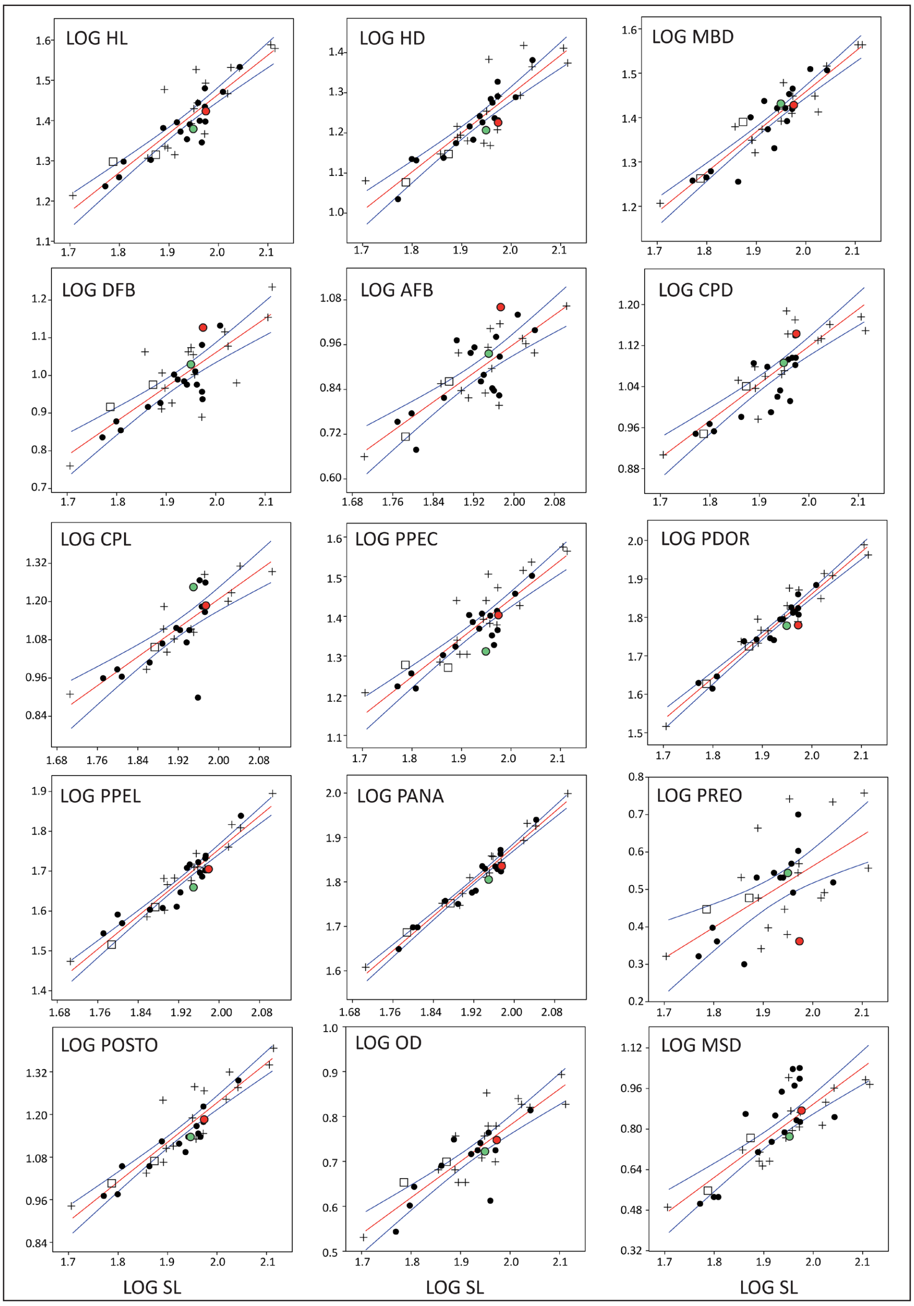


Fig. 9 - Scatterplots and regression lines (in red) with 95% confidence bands (in blue) of the relationship between the standard length (on x-axis) and each morphometric character (on y-axis) of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934). The lectotype of *T. madagascariensis* comb. n. (MNHN F.MAE112) and the holotype of '*Perleidus*' *piveteaui* (NHM P.19591) are marked with red and green circles, respectively; black circles = MSNM; cross = MNHN; square = MPUM..

0.61 to 0.96 (only preorbital length is 0.36; Tab. 4), indicating a good alignment of the points around the line and consequently suggesting a significant real dependence between the standard length and each morphometric character (all $p < 0.001$). Both the lectotype of *T. madagascariensis* comb. n. (MNHN F.MAE112), and the holotype of '*Perleidus*' *piveteaui* (NHM P.19591) fall within the cloud of points and near the regression lines, thereby suggesting that morphometric characters are not useful to distinguish two different species. There are no specimens falling more than three standard deviations from the mean, thereby suggesting homogeneous datasets.

Among the morphometric characters of *Teffichthys*, the preorbital length and the maximum scale depth show the most variation ($COV_{PREO} = 22.0$, $COV_{MSD} = 16.2$; Table 3), whereas the least variable characters are the predorsal, prepelvic and preanal distances ($COV_{PDOR} = 1.7$, $COV_{PPEL} = 1.8$, $COV_{PANA} = 1.0$). The number of pelvic- and anal-fin rays, and the pelvic-fin insertion are the most variable meristic characters in the sample ($COV_{PVFR} = 12.7$, $COV_{AFR} = 11.1$, $COV_{PFI} = 11.1$), whereas the number of caudal-fin rays and vertical scale rows are the least variable meristic characters ($COV_{CFR} = 0.0$, $COV_{VSR} = 2.3$). Coefficients of variation between count and length variables are not significantly different

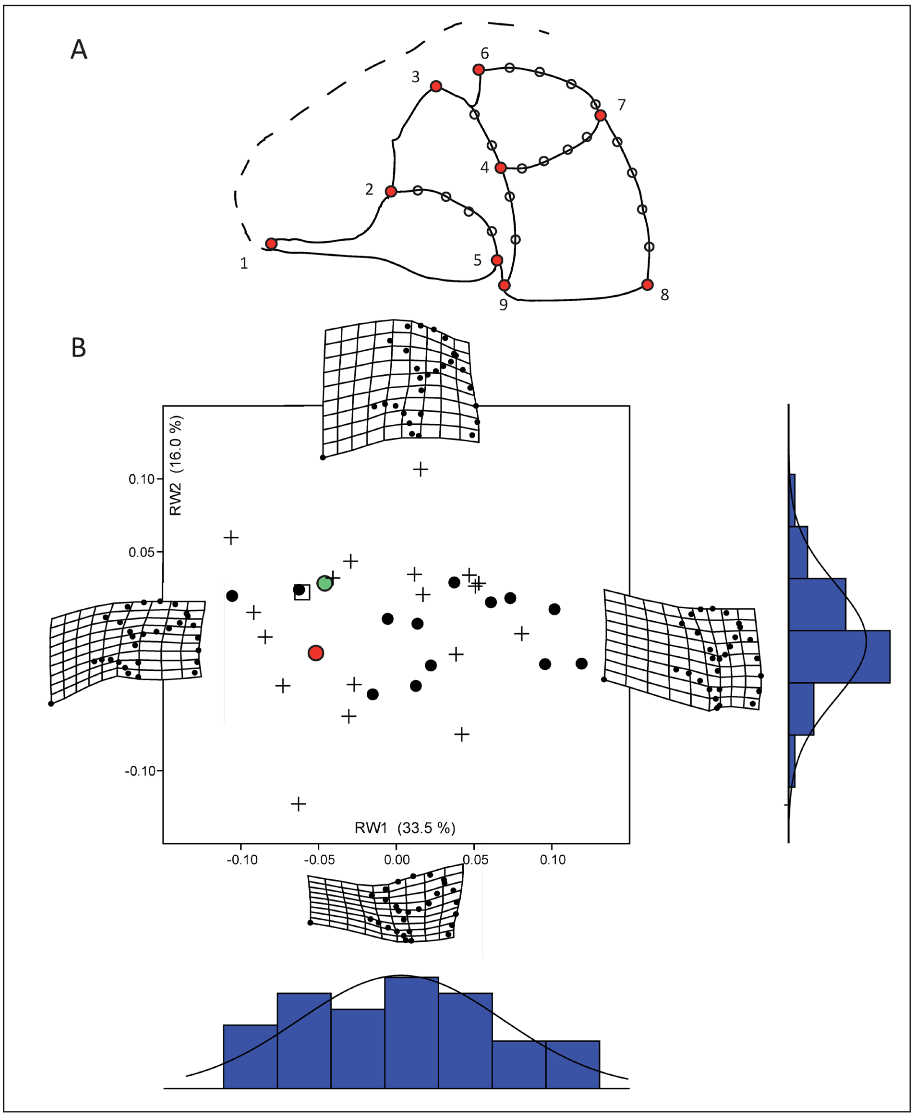


Fig. 10 - A) Landmarks and semi-landmarks configuration used for the analysis of the shape variation in the maxilla and opercular series of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934). Landmarks are represented by red circles, semilandmarks by open circles: 1 - anterior tip of maxilla; 2 - anterior joint between maxilla and preopercle; 3 - dorsalmost tip of preopercle; 4 - joint between preperclе, opercle and subopercle; 5 - posteriormost tip on posterior margin of maxilla; 6 - dorsalmost joint between opercle and dermohyal; 7 - posterior joint between opercle and subopercle; 8 - postero-ventral tip of subopercle; 9 - antero-ventral tip of subopercle. B) Morphospace plotted on the first two RW axes together accounting for about 50% of the overall shape variation. Deformation grids illustrate the shapes lying at extreme values along each axis. Note the proximity between the lectotype of *T. madagascariensis* comb. n. (MNHN F.MAE112, red circle) and the holotype of *'Perleidus' piveteaui* (NHM P.19591; green circle); black circles = MSNM; cross = MNHN; square = NHM. The histograms show the frequency of the points along each RW axis and their distribution suggests a unimodal (Gaussian) pattern.

(Mann-Whitney U-test: mean ranks 7.2 and 5.8, p = 0.39). The analysis of the entire morphometric and meristic dataset using the PCA and ANOSIM showed no significant differences between groups ("*P.*" *madagascariensis*, "*P.*" *piveteaui*, and "*P.*" sp.) defined a priori (p > 0.05) (see Supplementary material), therefore excluding the hypothesis of interspecific variation due to biometric parameters.

MORPHOSPACE ANALYSIS

According to Lehman (1952) one of the diagnostic differences between the supposed two Malagaysian species *'P.' madagascariensis* and *'P.' piveteaui* is the different ratio between the length and depth of maxilla, the presence of posterior margin of the maxilla articulating with the antero-ventral margin of the preopercle through a straight (in *'P.' madagascariensis*) or curved suture (in *'P.' piveteaui*), a forward inclined (in *'P.' madagascariensis*) or vertical preopercle (in *'P.' piveteaui*). Our re-examination of the types and other specimens shows that there is considerable morphological variation for these characters, and intermediate states are recognizable in the specimens, making difficult to distinguish two distinct groups in the sample.

The relative warp analysis produced 33 RW axes with the first two axes together explaining about 50% of the variation. The morphospace occupation showing the morphological variation of the maxillo-opercular apparatus of *Teffichthys* gen. n. in the whole sample is shown in Figs 10 and 11. The first two RWs describe the correlation between inclination of preopercle and the width of the opercular apparatus (Fig. 10). In particular, negative scores of the first RW axis (33.5% of variance) are related to specimens with a vertical preopercle,

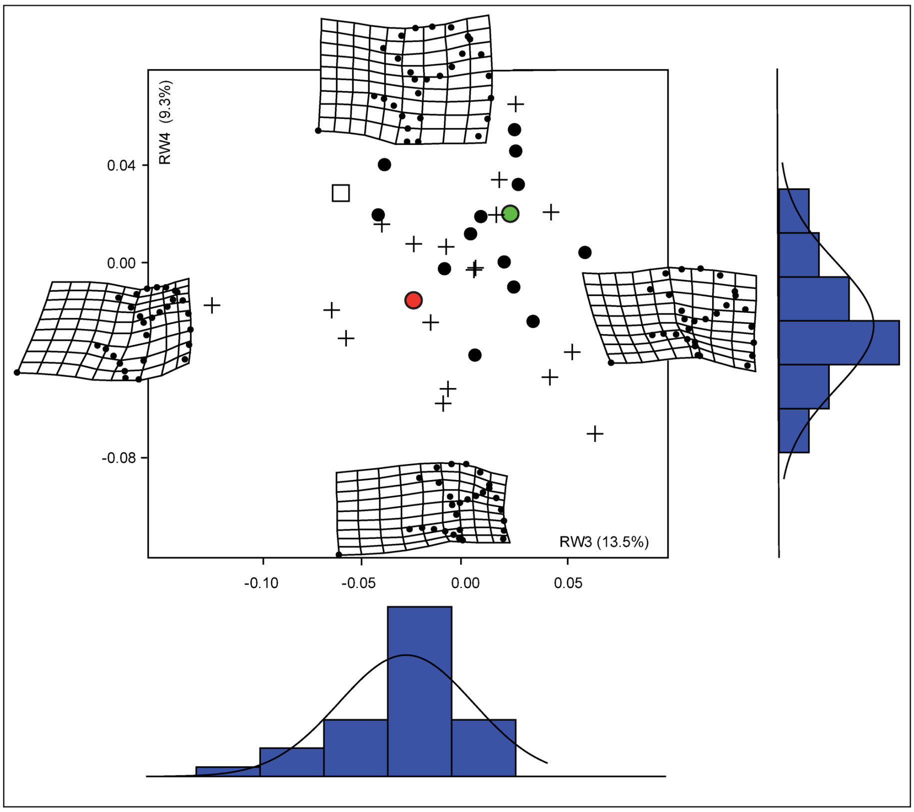


Fig. 11 - Morphospace plotted on the third and fourth RW axes together accounting for about 23% of the overall shape variation. Deformation grids illustrate the shapes lying at extreme values along each axis. The lectotype of *T. madagascariensis* (MNHN F.MAE112) is marked with a red circle; the holotype of *'Perleidus' piveteaui* (NHM P.19591) with a green circle; black circles = MSNM; cross = MNHN; square = NHM. The histograms show the frequency of the points along each RW axis, and their distribution suggests a unimodal (Gaussian) pattern.

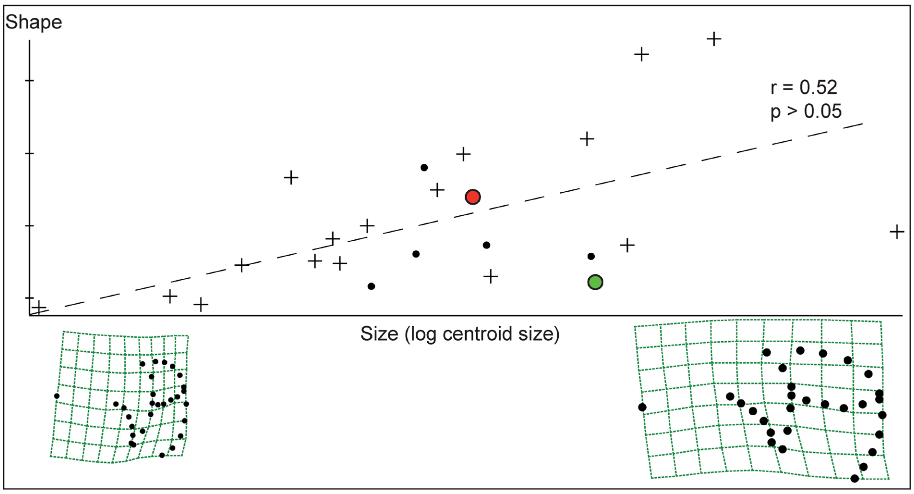
rounded posterior border of maxilla and large opercular series; on the contrary, on positive values of RW1 lie specimens with a slightly inclined forward preopercle, straight posterior border of maxilla and narrowed opercle and subopercle. On negative scores of RW2 (16.0 % of variance) lie specimens with inclined preopercle, straight posterior margin of maxilla and large opercular series, whereas on positive scores are specimens with vertical preopercle, curved margin of maxilla and narrowed operclular apparatus. The entire sample is normally distributed along the two main RW axes as shown by the respective histograms showing the distribution of specimens along the scores (Fig. 10B). Both the lectotype of *Teffichthys madagascariensis* comb. n. (MNHN F.MAE112), and the holotype of *'Perleidus' piveteaui* (NHM P.19591) fall near the center of the morphospace and very close to each other, therefore suggesting that, contrary to Lehman (1952), the morphology of the maxilla and the opercular series are not useful to distinguish two different morphotypes. The morphological meaning described by the other relative warp axes is more difficult to interpret, although the entire sample appears to be always normally distributed along the third and fourth RW axes (Fig. 11). The ANOSIM performed along all RW axes showed no significant differences in morphospace occupation between groups defined a priori ($p > 0.05$; see also Supplementary material), therefore suggesting that differences in shape cannot be related to interspecific diversity.

Morphometric character	Measurements as % of SL
Head length	27.6 - 30.9 (29.5)
Head depth	18.6 - 21.1 (20.0)
Maximum body depth	28.1 - 30.6 (29.2)
Dorsal-fin base	11.0 - 12.9 (11.8)
Anal-fin base	8.5 - 10.4 (9.3)
Caudal peduncle depth	12.9 - 14.7 (13.8)
Caudal peduncle length	14.8 - 16.7 (16.0)
Prepectoral distance	25.6 - 30.0 (28.0)
Predorsal distance	68.4 - 74.8 (71.7)
Prepelvic distance	53.6 - 59.0 (56.6)
Preanal distance	73.0 - 79.1 (76.1)
Preorbital length	3.0 - 4.3 (3.9)
Postorbital length	15.5 - 17.6 (16.9)
Orbit diameter	5.9 - 6.7 (6.3)
Maximum scale depth	6.3 - 8.3 (7.6)

Tab. 1 - Measurements as percentage of SL (mean values in parentheses) for *Teffichthys madagascariensis* comb. n. (Piveteau, 1934).

The PLS analysis (Fig. 12) detected a modera-

Fig. 12 - PLS regression between the shape of maxillo-opercular apparatus and size variation for a subset of 24 specimens. The x-axis represents the size from small (left) to large (right) specimens; the y-axis represents the shape variation. The lectotype of *T. madagascariensis* (MNHN F.MAE112) is marked with a red circle; the holotype of *'Perleidus' piveteaui* (NHM P.19591) with a green circle; black circles = MSNM; cross = MNHN. Extremes are illustrated by using deformation grid plots.



te although not significant link between shape and size (r = 0.52; p > 0.05). Small-sized individuals are mostly related to an inclined forward preopercle, maxilla with convex posterior margin, and narrow and high opercular apparatus; large specimens tend to have a more vertical preopercle, maxilla with straight posterior margin, and wider opercular series. In our opinion, the PLS analysis suggests that morphological variations of morphology of the maxilla, opercle and subopercle could be related, at least partially, to ontogeny, although we do not exclude that the effect of the taphonomic processes or individual variation (see Discussion) could have leaded the differences in morphologies within the sample.

DISCUSSION

Comparisons

The new taxon described herein shows a peculiar combination of characters which somewhat resembles the condition of 'subholostean' fishes in its cranial, squamation and fin patterns, but of the basal (non teleost) neopterygians for the caudal fin ossification pattern. The diagnostic characters of 'subholostean' fishes (Perleidiformes and Peltopleuriformes, among others) have already been remarked by several authors (e.g., Gardiner 1988; Gardiner & Schaeffer 1989; Bürgin 1992; Tintori & Lombardo 1996; Lombardo & Tintori 2004) who pointed out the peculiar combination of primitive and derived features that characterize these fishes. In particular, 'subholosteans' show derived characters in the postcranial skeleton respect to the 'paleonisciforms' (including caudal fin almost symmetrical with epaxial rays (semiheterocercal tail), and number of radials equal to lepidotrichia along most of the dorsal and anal fins) beside a primitive dermal skull bone pattern in which the maxilla is sutured to the preopercle and the interopercle is absent. Thus, *Teffichthys* gen. n. cannot be ascribed to 'subholostean' (and therefore to Perleidiformes) because of the absence of epaxial rays in the caudal fin. It is also to exclude the belonging of the new genus in the Neopterygii because of the absence of the derived cranial features characterizing this latter group, including more than four infraorbitals, presence of supramaxilla, maxilla separated from preopercle, and presence of interopercle (see e.g., Regan 1923; Schaeffer 1956; Patterson 1973; Xu et al. 2015). On the other hand, *Teffichthys* gen. n. cannot be considered among 'paleonisciforms', characterized by an antero-dorsally inclined preopercle and a fully heterocercal tail. Also, the new genus is different from *Ptycholepis* and related genera mainly in the cheek bones and in the squamation.

Osteological, meristic and morphological analyses presented herein, confirm the exclusion of the specimens examined from the genus *Perleidus* De Alessandri, 1910 and, consequently, support their attribution to a new genus, *Teffichthys* gen. n. Following the interpretation of Stensiö (1921, 1932), the examined specimens from Ankitokazo basin of Madagascar have been previously attributed to the genus *Perleidus* De Alessandri, 1910 by Piveteau (1934) and Lehman (1952) only on the basis of the primitive skull bone pattern, covering of ganoid scales, quite deep lateral flank scales, and fin rays only distally segmented; however, all of these studies did not consider the structure of the caudal fin, which is clearly abbreviate heterocercal in *T. madaga-*

	Pit-lines	Nasals separated by rostral	Spiraculars	Suborbitals	Supraorbitals	B.r.	P.-fin rays	D.-fin rays	A.-fin rays	Pel.-fin rays	C.-fin rays	Squamation formula
T. madagasariensis	present	present	present	present	4	5-6	12-13	14-15	11-12	7-8	20	D25/P13 A21 C37/ T40
T. lehmani	present	present	present	present	5	6	11	14	12	6-10	18-20	D23/P12 A21 C32/ T36
T. lutoensis	present	present	present	present	4	8	10-12	14	12-13	10	20-21	D28/P14 A25 C38/ T42
T. stoschiensis	present	present	present	present	5	?	?	?	?	?	?	?
T. woodwardi	present	present	present	present	2?	?	12-14	14-15	10	12-14	?	D27/P11 A? C?/T40
Paraperleidus	?	absent	absent	absent	3	?	?	?	?	?	?	?
Plesiofuro	present	present	absent	present	5	5	10-12	13-14	13-14	7-8	22	D28/P14 A25 C39/ T44
Plesioperleidus	absent	?	absent	absent	3	3-4	14-15	18	10	10	?	D?/P19 A? C?/T50

Tab. 2 - Summary of selected morphological features and meristic data used to discriminate *Teffichthys madagascariensis* comb. n. (Piveteau, 1934) from the other Early Triassic *Teffichthys* species, as well as from other similar actinopterygian genera. Data from Stensiö (1921, 1932), Antunes et al. (1990), Tong et al. (2006), Zhao & Lu (2007) and Xu et al. (2015). B.r.= Branchiostegal rays; P.= Pectoral; D.= Dorsal; A.= Anal; Pel.= Pelvic; C.= Caudal.

scariensis (see also Remarks). The anatomical analysis of *Teffichthys* gen. n. documented herein supports the hypothesis of Lombardo (2001) revealing the presence of a different combination of osteological characters useful to distinguish the new Malagaysian genus from *Perleidus*, as well as from other Early Triassic fishes as *Plesiofuro, Plesioperleidus* and *Paraperleidus*, all of them from China. The latter two taxa, although also wrongly considered as Perleidiformes, are in need of further comparison to understand their actual systematics meaning and relationships.

As documented herein, *Teffichthys madagascariensis* is characterized by the presence of three pit-lines on parietal, spiracular and an abbreviate heterocercal caudal fin. The presence of a single spiracular ossicle is diagnostic for *Teffichthys* gen. n. and it also characterizes all the other Early Triassic '*Perleidus*' species (see e.g., Stensiö 1929, 1932; Antunes et al. 1990). It is unclear if spiracular ossicles of *T. madagascariensis* comb. n. are homologous to those of 'paleoniscoid' fishes (e.g., Dietze 1999, 2000; Mickle et al. 2009; Mickle 2012). The fragmentation of this bone, or the remarkable individual variation in *T. madagascariensis* comb. n., might have induced Lehman (1952) to identify more than one spiracular in some of the specimens. A small element wedged between the opercle, the extrascapular, and the dermopterotic was identified as postspiracular by Lehman (1952) in a single specimen (NHM P.19591), although in our opinion it probably represents part of a fragmented dermopterotic or extrascapular (Figs 3A, 4D).

Teffichthys gen. n. differs from the other similar Early Triassic non-perleidiform genera (although unfortunately, most of them somewhat refers to '*Perleidus*' in their genus name) in its unique combination of osteological and meristic features (Tab. 2). Regarding the Early Triassic fish faunas from Southern China, Tong et al. (2006) ascribed all the Chinese species previously attributed to *Perleidus* to the genus *Plesioperleidus*, erected by Su & Li (1983). In particular, the species '*Perleidus*' *yangtzensis* (Su, 1981), '*Perleidus*' *eurylepidotrichia* (Liu et al., 2002) and *Zhangina yangtzensis* (Jin et al., 2003) are conclusively ascribed to the species *Plesioperleidus yangtzensis* (Su, 1981) in Tong et al. (2006). Jin et al. (2003) stated that also the two species from Madagascar *Perleidus* cf. *madagascariensis* and *Perleidus piveteaui* could not be attributed to the genus *Perleidus* and referred them to *Plesioperleidus jiangsuensis* (Qian et al., 1997). According to the diagnosis of Tong et al. (2006), *Plesioperleidus* is characterized by the presence of the supraorbital sensory canal traversing the entire length of parietal, pit-lines of parietal absent, no suborbital or spiracular ossicles, fewer than four supraorbital bones, three to four branchiostegals and

	Min	Max	Mean	Median	Variance	Standard deviation	Coefficient of variation
Standard length	51.1	129.3	87.5	89.1	280.3	16.7	-
Head length	16.4	38.7	25.9	24.9	29.8	5.5	3.4
Head depth	10.9	26.2	17.5	16.8	14.0	3.8	4.2
Maximum body depth	16.1	36.5	25.3	25.7	22.8	4.8	2.6
Dorsal-fin base	5.8	17.2	10.2	9.7	5.5	2.3	6.7
Anal-fin base	4.6	11.6	8.0	7.9	3.4	1.8	8.8
Caudal peduncle depth	8.1	15.4	11.8	12.0	3.9	2.0	4.0
Caudal peduncle length	8.0	20.6	13.7	13.1	12.8	3.6	7.3
Prepectoral distance	16.1	37.3	24.5	24.1	29.8	5.5	3.6
Predorsal distance	32.9	97.0	62.5	62.3	177.7	13.3	1.7
Prepelvic distance	29.8	78.2	48.8	49.6	99.3	10.0	1.8
Preanal distance	40.7	99.6	65.5	66.5	155.3	12.5	1.0
Preorbital length	2.0	5.7	3.3	3.2	0.9	1.0	22.0
Postorbital length	8.9	24.6	14.9	13.9	13.2	3.6	5.4
Orbit diameter	3.4	7.8	5.4	5.3	1.1	1.0	8.2
Maximum scale depth	3.1	10.9	6.7	6.5	4.6	2.1	16.2
Vertical scale rows	38	42	40.0	40.0	0.8	0.9	2.3
Horizontal scale rows	12	16	13.2	13.0	1.0	1.0	7.5
Dorsal-fin insertion	24	27	25.3	25.0	0.7	0.8	3.2
Anal-fin insertion	18	23	21.0	21.0	1.8	1.3	6.3
Pelvic-fin insertion	9	15	12.3	12.0	1.9	1.4	11.1
Pectoral-fin rays	11	15	12.6	12.0	1.1	1.1	8.4
Dorsal-fin rays	11	18	14.4	14.0	2.3	1.5	10.4
Anal-fin rays	10	15	11.8	11.5	1.7	1.3	11.1
Pelvic-fin rays	6	9	7.7	8.0	1.0	1.0	12.7
Caudal fin rays	20	20	20.0	20.0	0.0	0.0	0.0

Tab. 3 - Mean morphometric and meristic data for the examined specimens of *Teffichthys madagascariensis* comb. n. (Piveteau, 1934).

dorsal-ridge scales developed and spinous. All these characters differ significantly from *Teffichthys* gen. n. which instead possesses suborbitals, spiracular, three pit-lines on parietal, four supraorbitals, five to six branchiostegal rays. Concerning squamation, the dorsal-ridge scales in *Teffichthys* gen. n. are moderately developed, heart-shaped, but, unlike *Plesioperleidus* (see Tong et al. 2006), they are not spinous (see Fig. 4B-E).

The early actinopterygian fish *Plesiofuro* from the non-marine Early Triassic of Beishan, Gansu Province, China, previously referred to caturids by Su (1993), was recently redescribed by Xu et al. (2015) which placed it in a stem-group neopterygians together with *Perleidus*. However it must be pointed out that Xu et al. (2015) considered '*P.*' *madagascarensis*, and not the type species *P. altolepis*, not following Lombardo (2001), Jin et al. (2003), Tong et al. (2006). Thus, Xu et al. (2015) '*Perleidus*' is actually *Teffichthys*. *Plesiofuro* does not have any epaxial ray in the caudal fin as it is clearly shown in fig. 7C-D of Xu et al. (2015). The rays indicated by the arrows in fig. 7C being inserted ventrally to the body scale lobe are all those in the caudal fin in fig. 7D. Anyway, in *Plesiofuro* the supraorbital sensory canal runs for about the half of the length of parietal, and three pit-lines are posteriorly displaced in this bone. On the contrary, *Teffichthys* has three pit-lines uniformly located along the anterior, lateral and posterior margins of the parietal, with the sensory canal coming from the frontal that ends on the anterior pit-line. Moreover, *Plesiofuro* differs from our specimens by lacking of spiracular, and by having different meristic counts (see Tab. 2).

The genus *Paraperleidus* was erected by Zhao & Lu (2007) based on a single specimen from the Early Triassic of Changxing, China. The authors placed this genus within Perleididae due to its primitive skull bone pattern (preopercle nearly vertical, skull bones ornamented, opercle smaller than subopercle, maxilla 'paleoniscoid'-like and posttemporals widely separated), without any indication of the caudal-fin ossification pattern which is on the other hand clearly abbreviated heterocercal (Zhao & Lu 2007, fig. 1). Thus, *Paraperleidus* cannot be considered a Perleididae but also it can be easily separated from *Teffichthys* mainly for the presence of nasals medially in contact and not separated by the rostral, absence of suborbital and spiracular, and for the presence of a supraorbital sensory canal running almost entirely the length of the parietals.

The phylogenetic relationships of *Teffichthys* gen. n. within the early actinopterygians were already investigated by Xu et al. (2015) who erroneously used '*Perleidus*' *madagascariensis* as representative for Perleididae, but coding correctly for it the absence of epaxial rays on caudal fin. According to the analysis of Xu et al. (2015) *Teffichthys* is therefore placed as a stem-group neopterygian, phylogenetically distant from the crown-group Neopterygii (including Ginglymodi, Halecomorphi and Teleostei), because of the absence of a series of derived features characterizing the most derived neopterygian fishes (e.g., more than four infraorbitals, presence of supramaxilla, interopercle and ossified vertebral centra). However, according to their study *Plesiofuro*, *Pseudobeaconia*, *Peltoperleidus* and *Teffichthys*, and the most derived neopterygians form an unresolved polytomy sharing two synapomorphies that have been linked to an increased maneuverability during the swimming (see Schaeffer 1956), (1) the presence of median fins with distally segmented rays and (2) pterygiophores supporting an equal number of median-fin rays. However, we have to point out that Xu et al. (2015) appears not so sound as the choice of the taxa (and characters) is at least curious, *Plesiofuro* being nested in the suholosteans when we demonstrate it is not possible lacking the hemiheterocercal tail.

A detailed revision of the other Early Triassic '*Perleidus*' species would be necessary to properly investigate the relationships of *Teffichthys* within the early actinopterygians. From this perspective, the Early Triassic taxa '*Perleidus*' *woodwardi*, '*P.*' *stoschiensis*, '*P.*' *lutoensis* and '*P.*' *lehmani*, which show similar skull, squamation and caudal-fin ossification patterns as *T. madagascariensis* comb. n., and differ only for the meristic counts (Tab. 2), although in need of revision, can be confidently ascribed to the new genus described herein, allowing thus to definitively exclude the presence of *Perleidus* as well as Perleidiformes, in the Induan and Smithian (early Olenekian) Triassic. Most of the characteristic taxa of the TEFF faunas disappeared at the Smithian/Spathian boundary, and only a few long lasting, almost cosmopolitan genera such as *Saurichthys*, *Birgeria* and

Variable log(y)	**Slope (m)**	**Intercept (b)**	**Coefficient of determination (r^2)**	**95% CI on m**	**95% CI on b**
Head length	0.97 ± 0.08	-0.48 ± 0.16	0.79	0.84 1.09	-0.70 -0.22
Head depth	0.97 ± 0.09	-0.64 ± 0.07	0.78	0.78 1.11	-0.91 -0.28
Maximum body depth	0.91 ± 0.06	-0.35 ± 0.12	0.85	0.80 1.01	-0.55 -0.16
Dorsal-fin base	0.91 ± 0.12	-0.76 ± 0.23	0.65	0.73 1.15	-1.22 -0.42
Anal-fin base	0.97 ± 0.14	-0.98 ± 0.26	0.61	0.78 1.18	-1.39 -0.62
Caudal peduncle depth	0.73 ± 0.08	-0.33 ± 0.16	0.71	0.60 0.83	-0.53 -0.09
Caudal peduncle length	0.13 ± 0.16	-1.06 ± 0.31	0.64	0.98 1.32	-1.41 -0.60
Prepectoral distance	0.98 ± 0.17	-0.51 ± 0.17	0.78	0.83 1.11	-0.77 -0.22
Predorsal distance	1.09 ± 0.05	-0.32 ± 0.10	0.93	1.02 1.19	-0.51 -0.18
Prepelvic distance	1.05 ± 0.06	-0.33 ± 0.11	0.91	0.91 1.16	-0.55 -0.06
Preanal distance	0.98 ± 0.04	-0.07 ± 0.07	0.96	0.90 1.04	-0.20 -0.02
Preorbital length	0.82 ± 0.20	-1.08 ± 0.38	0.36	0.49 1.15	-1.72 -0.45
Postorbital length	1.11 ± 0.09	-0.99 ± 0.17	0.83	0.96 1.23	-1.22 -0.69
Orbit diameter	0.81 ± 0.09	-0.83 ± 0.17	0.73	0.68 0.96	-1.13 -0.58
Maximum scale depth	1.45 ± 0.18	-1.99 ± 0.34	0.66	1.10 1.73	-2.55 -1.34

Tab. 4 - Relationships between standard length (log x) and the various morphometric characters (log y) using least squares regression for *Teffichthys madagascariensis* comb n. (Piveteau, 1934). All $p < 0.001$.

Bobasatrania went across it (Tintori et al. 2014). After that event, actinopterygian fishes went through a slow recovery in the Spathian, where the first real Perleidiformes appeared (Sun et al. 2013), before the Anisian blooming.

INTRASPECIFIC VARIATION IN *TEFFICHTHYS* GEN. N.

The study of phenotypic variations within a population is one of the main challenges for paleobiologists in order to avoid the taxon over-splitting (Labandeira & Hughes 1994; Hughes & Labandeira 1995; Weitschat 2008). In our case study, Lehman (1952) identified a second species of '*Perleidus*' ('*P.*' *piveteaui*) in the Early Triassic of Madagascar, distinguishing it from '*P.*' *madagascariensis* primarily based on the differences in shape and proportions of the maxilla and opercular apparatus, without any meristic difference. The analysis of 45 specimens from the Early Triassic of the Ankitokazo basin documented herein, has revealed a great homogeneity in morphometric and meristic features and, at the same time, a remarkable morphological variation within the sample, which can be explained as due to intraspecific variation. Grande (2004) recognized two types of intraspecific variation, ontogenetic (due to ontogenetic variations of osteological characters) and individual (due to sexual dimorphism, polymorphism, anomalies, etc.). In *T. madagascariensis* comb. n. we identified both the types of variation.

Frequency histograms for morphometric and meristic data appear normally distributed with a clear domination of intermediate forms and rare extremes, thereby following a unimodal distribution (Gaussian), whereas the least square regression analyses demonstrated a real significant dependence between standard length and each morphometric character (see Figs 7-9; Tab. 4). The biometrical analyses shows that the morphological variations for all of these characters are continuous and intermediate states can be recognizable among the specimens making impossible to separate the entire sample into discrete groups. Several studies suggest that if the morphological variation of a character is Gaussian in nature, we can assume that all specimens belong to a single genetically linked population (see e.g., Dagys et al. 1999; Dagys 2001; Weitschat 2008; Marramà & Carnevale 2015; Sferco et al. 2015). The continuity of the morphological variations and the difficulty to split the sample into different group based on osteological characters were also detected by the morphospace analysis which did not detect clustering in the sample (see Figs 10-11). On the contrary, geometric morphometrics has shown a certain relationship between size and shape of the structures analyzed, thereby suggesting that morphological variation could be related, at least in part, to ontogenetic changes, and not to interspecific variation. Moreover, the comparison of juveniles and adults showed the presence of other osteological characters subject to ontogenetic variation. For example, in small-sized specimens the dermal bones of the skull have a feeble ornamentation whereas in the adults ridges and tubercles are more accentuated; the serration of the posterior margin of the scales is more evident in large specimens, whereas the marginal ornamentation of scales is weak or absent in small individuals; the squamation of juvenile specimens is incomplete, lacking one or two horizontal scale rows at the base of the dorsal and anal fins. Some of these differences between juvenile and adult individuals of *T. madagascariensis* comb. n. were also reported in several other early actinopterygians (see e.g., Dietze 1999; Tintori & Lombardo 1999; Lombardo 2001; Sferco et al. 2015).

Although morphometric, meristic and morphological characters suggest a homogenous sample and do not allow to distinguish more than one species, other features described for *T. madagascariensis* comb. n. were instead recognized as the product of individual variation. Individual variation was correlated with several factors in actinopterygians, including life style, sex, habitat, temperature and latitude (Frey et al. 2016). In *Teffichthys* gen. n. these characters, including the fusion of the parietal bones, the different morphology of the sutures between cranial bones, the depth of the anteriormost flank scales and the differences in the meristic counts, are consistent with the intraspecific variation already described in other actinopterygians. In particular, the morphological variation of anteriormost lateral line scale among specimens detected through the scale ratio (SR) between the maximum depth of the first lateral line scale and the scale immediately below, although not normally distributed, appears to be continuous and can-

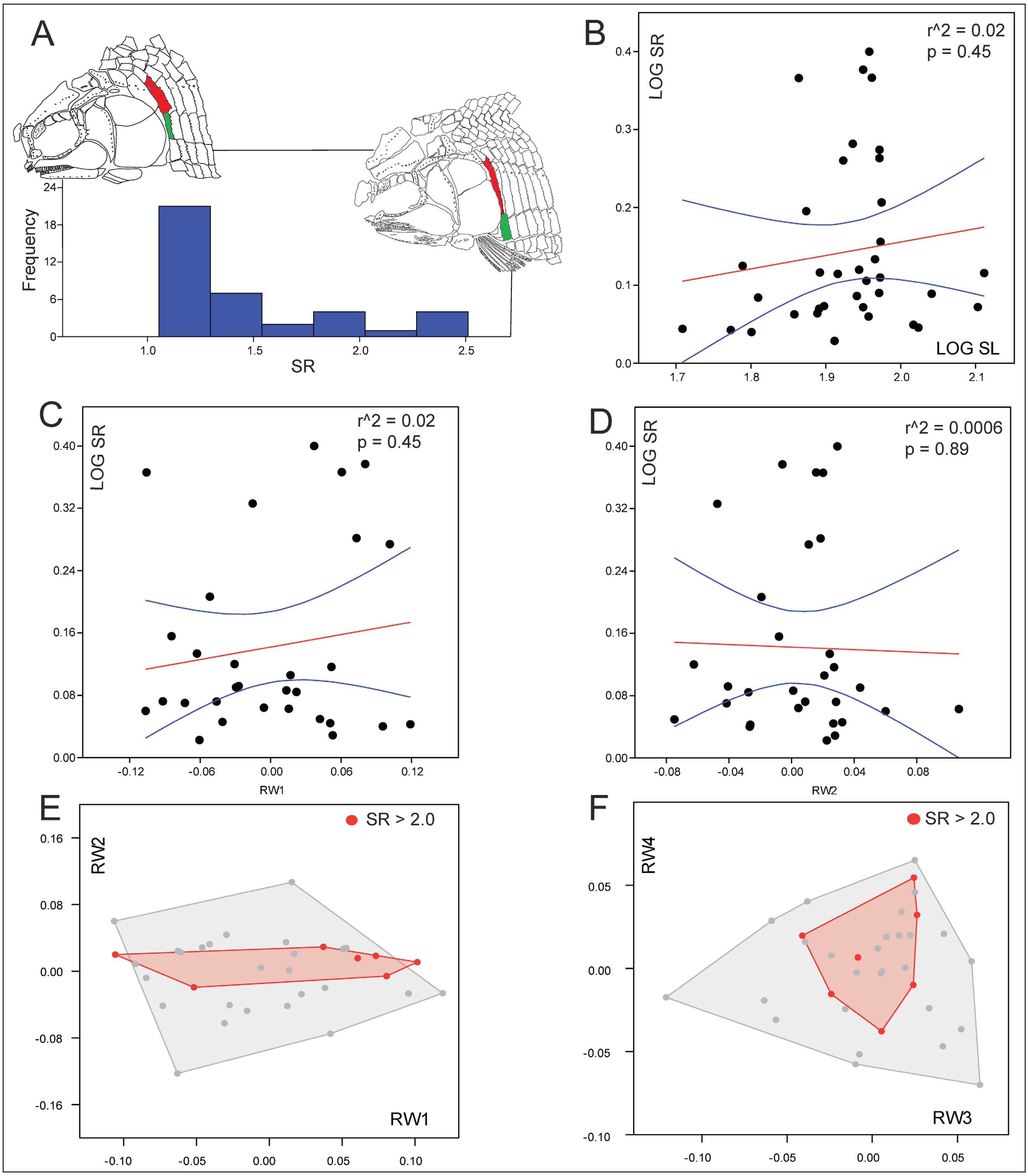


Fig. 13 - A) Histogram showing the frequency of specimens based on the scale ratio (SR) variation between the maximum depth of the first lateral line scale (in red) and the scale immediately below (in green). Note that the distribution of the frequencies is continuous with a main peak around the unit. B) Partial least square regression between the size (log SL) and scale ratio (log SR). C-D) Partial least square regressions between the first two RW axes and the scale ratio (log SR). E-F) Morphospaces plotted on the first four RW axes showing the distribution of the specimens with high scale ratio (RS > 2.0).

not be used to separate different morphotypes (Fig. 13A). Moreover, we did not detect any significant relationship between the scale ratio and size (Fig. 13B), or shape of the maxilla and opercular apparatus (Fig. 13C-D) ($p > 0.05$), and the specimens with $SR > 2.0$ spread throughout the morphospace

(Fig. 13E-F). In our opinion, since no other characters are useful to distinguish the specimens with high lateral line scales from those with low ones, this feature can be considered an intraspecific variation typical of *Teffichthys* gen. n.. The individual variation is not rare in Paleozoic and Mesozoic fishes and several cases are well-documented for example in *Australosomus*, *Dapedium*, *Ikechaoamia*, *Malingichthys*, *Paramblypterus*, *Peltoperleidus*, *Prohalecites*, *Pteronisculus*, *Saurichthys*, *Sinamia*, and parasemionotids (see Stensio 1935; Lehman 1952; Patterson 1973; Su 1973; Zhang & Zhang 1980; Olsen 1984; Jain 1985; Tintori 1990b; Bürgin 1992; Dietze 1999, 2000; Thies & Hauff 2011; Xu et al. 2014; Tintori et al. 2015) suggesting that polymorphism that sometimes resulted in the species over-splitting in early actinopterygian fishes also led to the identification of more than one species of *Teffichthys* gen. n. in the Early Triassic of Madagascar.

CONCLUSIONS

Detailed osteological, morphometric and meristic analyses revealed a remarkable intraspecific variation in *Teffichthys* gen. n., suggesting that '*Perleidus*' *piveteaui* is to be considered as a junior synonym of '*Perleidus*' *madagascariensis*. Since the generic assignation is considered erroneous since Lombardo (2001), the new combination *Teffichthys madagascariensis* n. comb. is therefore proposed. Our analysis confirmed the presence of several important differences in the anatomy of the skull and the caudal fin between *Perleidus* De Alessandri, 1910 and *Teffichthys* gen. n., as well as between these two genera and coeval Chinese taxa such as *Plesioperleidus, Paraperleidus,* and *Plesiofuro*. For these reasons, we exclude the presence of *Perleidus* in the Lower Triassic of Madagascar and China. We also suggest that the other Early Triassic '*Perleidus*' species from Spitsbergen, Greenland, Canada and Angola, although pending detailed revisions, can be considered as belonging to *Teffichthys* gen. n. and, therefore, definitively excluding the presence of *Perleidus* in all TEFF assemblages, the oldest actual perleidid being the Spathian *Chaohuperleidus* from south-east China (Sun et al. 2013).

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