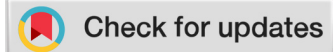


ORIGINAL RESEARCH



Phyllothea douroensis sp. nov., a new equisetalean fossil-species from the Douro Carboniferous Basin (Upper Pennsylvanian; NW Portugal): palaeobiogeographical, systematic and evolutionary implications

Catarina Barbosa

Department of Geosciences, University of Évora, Largo dos Colegiais 2, 7000-645 Évora, Portugal.
ORCID: <https://orcid.org/0000-0003-1179-6553>

Pedro Correia

Geosciences Center, University of Coimbra, Largo Marquês de Pombal, 3000-272 Coimbra, Portugal.
Corresponding author. Email: pedro.correia@dct.uc.pt, ORCID: <https://orcid.org/0000-0002-0573-7138>

João Muchagata

Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP), Praça Gomes Teixeira, 4099-002 Porto, Portugal. ORCID:

Rúben Domingos

GEOBIOTEC, Earth Sciences Department, NOVA School of Science and Technology, Campus de Caparica, P-2829 516 Caparica, Portugal. ORCID: <https://orcid.org/0000-0002-0373-9869>

Artur A. Sá

Department of Geology, University of Trás-os-Montes e Alto Douro, 5001-801 Vila Real, Portugal. ORCID: <http://orcid.org/0000-0003-0811-2413>

© The Author(s), 2022

ABSTRACT

The first occurrence of the fossil-genus *Phyllothea* (Equisetales) from the Carboniferous of Portugal is documented and its palaeobiogeographical, systematic and evolutionary significance is assessed. In this paper, we described this new equisetalean fossil as new species, *Phyllothea douroensis* sp. nov., found in the Douro Carboniferous Basin (lower Stephanian C/lower Gzhelian, Upper Pennsylvanian), in northwestern Portugal. *P. douroensis* sp. nov. represents a convergent form of Phyllothecaceae sensu lato (comprises the Angaran Tchernoviaceae and the Gondwanan Gondwanostachyaceae) with closer affinities to Euramerican floral province.

ARTICLE HISTORY

Received: 1-11-2021
Revised: 17-12-2021
Accepted: 25-01-2022

KEYWORDS

Phytogeographic provinces (Floral Realms);
Convergent evolution;
Phyllothea;
Equisetales;
Douro Carboniferous Basin;
Lower Gzhelian (Upper Pennsylvanian)

1 Introduction

THE GLOBAL-SCALE changes in the Earth's climate of the late Palaeozoic due to the formation of supercontinent Pangaea had a key role for the global distribution

of floras. These late Palaeozoic floras were segregated into four major phytogeographic provinces (Floral Realms) – Angara, Euramerica, Cathaysia and Gondwana (e.g., Oshurkova, 1996; Vai, 2003; Wagner, 2004; Sunderlin, 2010;

Cocks & Torsvik, 2011; Pfefferkorn & Wang, 2016; Correia & Murphy, 2020; Correia et al., 2021). The different “Floral Realms” show clear differences in their terrestrial plants which colonized in different palaeoclimates (e.g., Oshurkova, 1996; Wagner, 2004). Although they shared similar palaeoecologies, these palaeoprovinces developed different floral assemblages and coal forming plants (e.g., Oshurkova, 1996; Wagner, 2004). More conclusive floral signatures are based on a large number of species and genera replaced by endemic taxa in each of four floristic provinces (e.g., Oshurkova, 1996; Vai, 2003; Wagner, 2004; Srivastava & Agnihotri, 2010; Correia & Murphy, 2020; Correia et al., 2021).

However, several convergent plant forms with strong morphological similarity have been documented among the different palaeoprovinces (e.g., Boureau, 1964; Naugolnykh, 2002; Boardmann & Iannuzzi, 2010; Srivastava & Agnihotri, 2010; Boardman et al., 2016; Correia et al., 2021). The late Palaeozoic equisetalean *Phyllothea* (sensu Brongniart, 1828) is a fossil-genus that has been described for several plant groups of the Equisetales of similar foliage (*Phyllothea*-type) with different phylogenetic affinities (e.g., Meyen, 1967, 1969, 1971, 1982, 1987; Cúneo & Escapa, 2006; Naugolnykh, 2002; Taylor et al., 2009; Boardmann & Iannuzzi, 2010; Srivastava & Agnihotri, 2010; Boardman et al., 2016; Correia et al., 2021). *Phyllothea* is a cosmopolitan taxon that was widespread across the Angaran and Gondwanan floral provinces during Carboniferous and Permian times (e.g., Townrow, 1955; Boureau, 1964; Meyen, 1969, 1971, 1982; Oshurkova, 1996; Mcloughlin et al., 2005; Cúneo & Escapa, 2006; Taylor et al., 2009; Srivastava & Agnihotri, 2010; Prevec et al., 2010; Boardman et al., 2016; Correia et al., 2021). By contrast, there are other equisetaleans that occur only in restricted regions or in a specific province because of the restricted environmental, climatic and ecological conditions in which these plants lived. Such

conditions led to origin to many endemic forms with singular morphological characteristics (e.g., Boureau, 1964; Verbitskaya & Radchenko, 1968; Oshurkova, 1996; Naugolnykh, 2002; Weber, 2008; Correia et al., 2021).

In this paper, we report an enigmatic equisetalean fossil from Euramerican province with similar floral (morphological) characteristics to Gondwanan and Angaran provinces, found in the Douro Carboniferous Basin (DCB; lower Stephanian C/Gzhelian, Upper Pennsylvanian) in northwestern Portugal (Fig. 1). Here, we describe this new fossil as *Phyllothea*-like and assess its palaeobiogeographical, systematic and evolutionary significance with the potential floral endemism present in the DCB.

2 Geological and palaeontological background

The DCB is a narrow (typically less than 1 km wide) sedimentary basin that occurs within the Douro-Beira Carboniferous Trough (DBCT), which is located within the Central Iberian Zone of the Variscan (or Hercynian) Chain of the Iberian Massif in northwestern Portugal (Fig. 1). The DBCT strikes approximately in a northwest to southeast direction and extends about 85 km from the localities of São Pedro Fins (Maia, NE Porto) to Janarde (Arouca). The DBCT is generally interpreted as a narrow pull-apart basin with a sinistral strike-slip component (Pinto de Jesus, 2001, 2003). Within the DBCT, there are several, well-documented exposures of terrestrial strata that were deposited during the Carboniferous. These deposits range in age from middle Bashkirian to Moscovian (equivalent to Westphalian in regional chronostratigraphy) to upper Gzhelian (equivalent to Stephanian C/lower Autunian in regional chronostratigraphy).

Strata in the intramontane DCB consist of terrestrial, syntectonic deposits of early Stephanian C (early Gzhelian) age (Lemos de Sousa & Wagner, 1983; Wagner, 1983; Domingos et al., 1983;

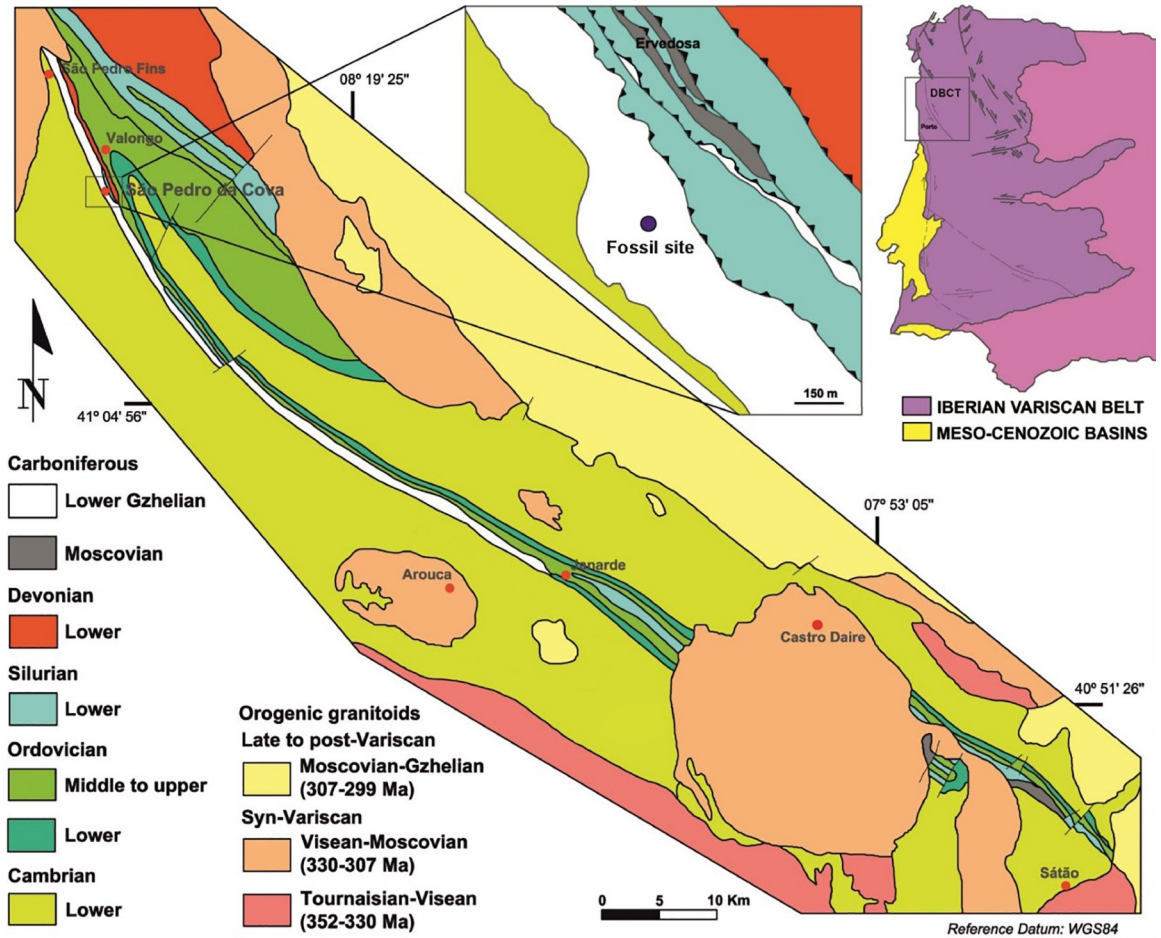


Figure 1. Regional geological setting of the Douro Carboniferous Basin (lower Stephanian C/lower Gzhelian, NW of Portugal). Geological map showing detailed geology of the São Pedro da Cova region with fossil site where was found *Phyllotheca douroensis* sp. nov. Modified from Correia et al. (2016, fig. 1).

Pinto de Jesus, 2001, 2003). Toward the southwest, the basal strata unconformably overlie a Neoproterozoic to middle Cambrian sequence known as the Schist-Greywacke Complex. Toward the northeast, the upper strata of the DCB are truncated by a reverse fault that placed the Silurian to Devonian sequence of the Valongo Anticline over the DCB strata (Domingos et al., 1983; Pinto de Jesus, 2001, 2003).

The context for interpreting the new equisetalean fossil reported herein is provided by associated flora and fauna that occur in deposits with intramontane characteristics. These deposits are described in detail by Wagner and Lemos de Sousa (1983) and Correia et al.

(2016, 2018) who documented dryland floral elements in the DCB such as walcchian conifers *Ernestiodendron filiciforme* (Schlotheim ex Sternberg) Florin, cf. *Culmitzschia frondosa* (Renault) var. *zeilleri* (Florin) Clement-Westerhof and *Culmitzschia parvifolia* (Florin) Kerp et Clement-Westerhof, dicranophyllaleans *Dicranophyllum gallicum* Grand'Eury and *Dicranophyllum lusitanicum* Heer, cordaitalean *Cordaites*, and the cycadopsid *Lesleya iberiensis* Correia et al. The intramontane deposits of DCB are also characterised by the presence of the non-marine and limnic bivalves *Anthraconaia lusitanica* (Teixeira) Eagar and *Anthraconaia? altissima* Eagar (Eagar, 1983).

3 Material and methods

3.1 Locality and fossil material

The *Phyllotheca*-like fossil (Fig. 3A) was discovered in an excavation (outcrop location: 41°09'44.65" N, 08°30'25.73" W) during fieldwork in 2010 in the São Pedro da Cova region, in the DCB (Fig. 1).

Here, we describe it as a new species of *Phyllotheca*. The fossil material consists of a single specimen (holotype) and is preserved as adpression (compression/impression; sensu Shute & Cleal, 1996) in a laminated shale bed. This lithology contains several layers very rich in fossils with well-preserved plant and animal remains (Fig. 2B).

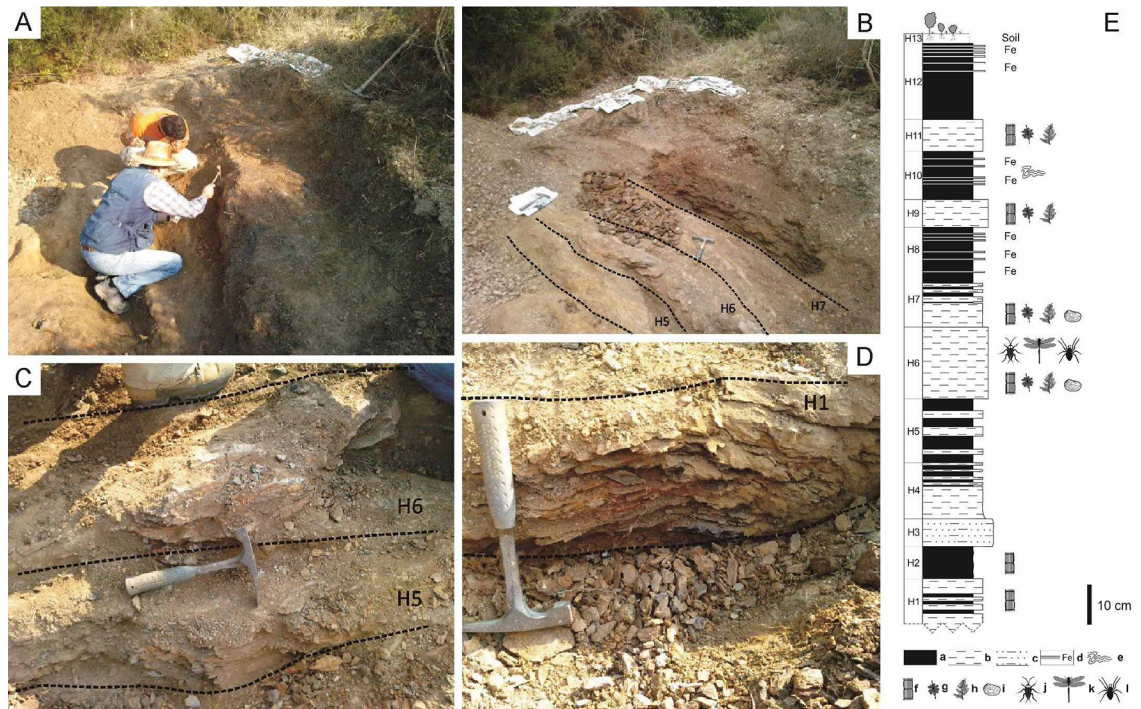


Figure 2. Lower Gzhelian outcrops of the Sao Pedro da Cova region, Douro Carboniferous Basin, north-western Portugal. (A) Description of the different horizons of the log; (B) Samples collection of the different horizons; (C). H5 and H6 horizons rich in plant fossils, containing some very rare faunal fossils such as non-marine bivalves, insects and arachnids; (D). Shale levels containing trunks of *Calamites* interlayered with oxidised iron levels. Excavation works during fieldwork in 2010. (E) Stratigraphic log of the lower Gzhelian outcrops of the occurrence of *Phyllotheca douroensis* sp. nov., in Sao Pedro da Cova region. (a) Coal-bearing shale. (b) Fossil-bearing shale. (c) Silt-rich shale. (d) Ferruginous (clay with oxidised iron) shale. (e) Levels with tectonic deformation. (f) *Calamites*-rich levels. (g) *Annularia*-rich levels. (h) Pteridosperms and ferns. (i) Non-marine bivalves. (j) *Lusitanaura covensis* Loureiro et al., 2010. (k) Palaeodictyoptera (e.g., *Stenodictya lusitanica* Correia et al., 2014 and Dictyoptera (blattodeans) insects). (l) *Aphantomartus pustulatus* (Scudder) Rössler. Modified from Correia et al. (2013, fig. 2).

The fossil site (Fig. 2A) preserves various fossiliferous levels containing many remains of plant and animal fossils. The new *Phyllotheca* species was found together with a diverse flora with several fossil-taxa belonging to ferns (e.g., *Cyathocarpus* Weiss, *Lobopteris* Wagner,

Acitheca Schimper, *Oligocarpia* Göppert, *Asterotheca* Presl ex Corda, *Stelatheca* Danzé, *Spiropteris* Schimper), pteridosperms (e.g., *Douropteris* Correia et al., *Eusphenopteris* Gothan ex Simson-Scharold non Kidston, *Callipteridium* (Weiss) Zeiller, *Pseudomariopteris*

Danzé-Corsin, *Neuropteris* (Brongniart) von Sternberg, *Sphenopteris* (Brongniart) von Sternberg, *Dicksoniites* Sterzel, *Telangium* Benson, *Cyclopteris* Brongniart), and calamitaleans (e.g., *Calamites* Suckow, *Asterophyllites* Brongniart, *Annularia* von Sternberg, *Calamostachys* Schimper, *Sphenophyllum* Brongniart (Correia et al., 2019a, b). The *Phyllothea*-like fossil (Fig. 3A) occurs in association with other equisetaleans (e.g., *Annularia noronhai* Correia et al., 2019b) and many fern and pteridosperm taxa (e.g., *Douropteris alvarezii* Correia et al., 2019a) found in the H6 horizon (Fig. 2B, C, E).

The faunal assemblage is also composed of rare animal elements, such as myriapods, arachnids (*Aphantomartus pustulatus* (Scudder) Rössler), eurypterids (*Adelophthalmus* sp.) and insects (dictyoptera and palaeodictyoptera), and includes non-marine bivalves likely belonging to the species *Anthraconaia lusitanica* Teixeira (e.g., Loureiro et al., 2010; Correia et al., 2013, 2014a, b; Correia et al., 2019a, b; Fig. 2B). The occurrence of these non-marine bivalves indicates that the plants and arthropods lived at the interface between fluvio-lacustrine freshwater environments within an intramontane basin (Correia et al., 2016, 2019a, b).

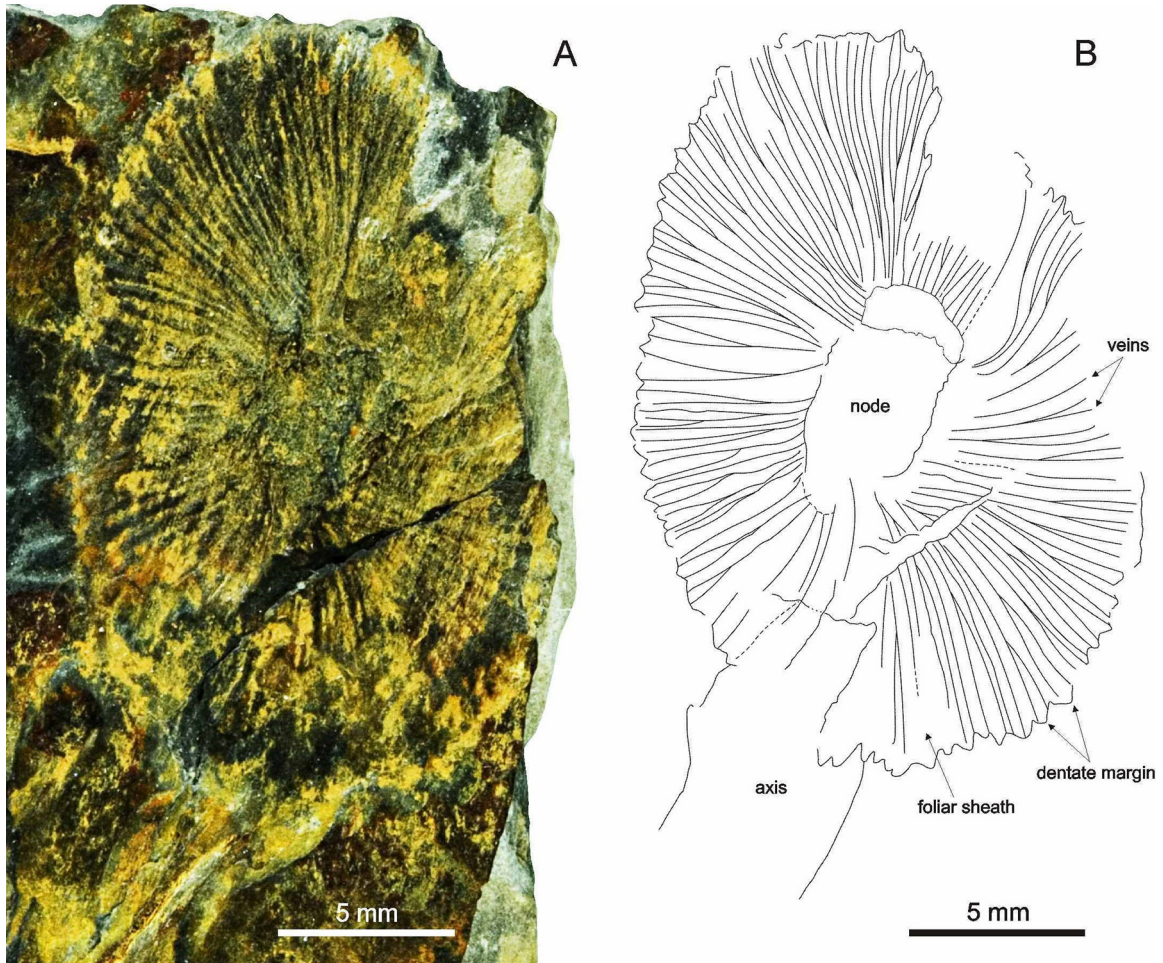


Figure 3. *Phyllothea douroensis* sp. nov., São Pedro da Cova region, Douro Carboniferous Basin, north-western Portugal. (A) Holotype specimen (MHNCUP/PAB-130919) characterised by a basal? leaf whorl attached to a broad axis. (B) Camera-lucida hand drawing of holotype highlighting the large and well-developed disc shaped foliar sheath of the new species.

3.2 Sample preparation and repository

The holotype specimen was cleaned either manually or mechanically with a compressed air and electric vibrotool, and drawn using a camera lucida to help with the taxonomic evaluation. It is stored in the Museu de História Natural e da Ciência da Universidade do Porto (MHNC-UP; Portugal).

4 Systematic palaeobotany

Division **Sphenophyta**

Class **Equisetopsida** Agardh, 1825

(Subclass **Equisetidae**)

Order **Equisetales** DC. ex Berchtold &
Presl, 1820

Family **Phyllothecaceae** sensu lato
Brongniart, 1828

(**Phyllothecaceae** sensu stricto ≡
Gondwanostachyaceae Meyen, 1969)

Genus **Phyllothea** Brongniart, 1828
emend. Townrow, 1955

1828 *Phyllothea* Brongniart, p. 152.

1955 *Phyllothea* Brongniart emend.

Townrow, p. 39–40.

Type species: *Phyllothea australis*
Brongniart, 1828 emend. Townrow, 1955;
type horizon unknown, Hawkesbury River,
Sydney Basin, New South Wales, Australia
(McLoughlin, 1992; McLoughlin et al.,
2005).

Generic diagnosis: See Townrow
(1955, p. 39–40; see also Boureau, 1964,
p. 392–396).

Distribution of the genus: Cosmopolitan
genus; late Carboniferous to Early
Cretaceous (e.g., Boureau, 1964; Maheshwari,
1974; Anderson & Anderson, 1985;
McLoughlin, 1992).

Phyllothea douroensis sp. nov.

Holotype: MHNCUP/PAB-130919 (Fig. 3A).

Type locality: São Pedro da Cova region,
DCB, northwestern Portugal (Fig. 1).

Stratigraphic age: Early Stephanian
C (middle Gzhelian, ca. 303 Ma), Late
Pennsylvanian.

Type horizon: Compressed and laminated
grey shales; horizon H6 (Fig. 2B, C, E).

Etymology: The specific epithet “*douroensis*”
refers to the Douro Carboniferous Basin
from which the fossil was collected.

Diagnosis: Leaf whorl with a single,
large and well-developed foliar sheath,
totally opened in disc shape, and basally
attached to a broad axis; densely covered
with simple to divided veins; veins mainly
divided two times (rarely thrice); sheath
margins irregular and entirely dentate;
small and asymmetrical dentate margins.

Description of the holotype: The
holotype MHNCUP/PAB-130919 (Fig. 3A)
consists of a nearly complete leaf whorl,
partially fused into a single, large and
well-developed disc shaped foliar sheath
which is attached to a broad axis. The
leafy axis has a width of about 5 mm and
is poorly preserved. The foliar sheath is
large of 4.5–7.5 mm in width and has a
total length of about 22 mm. The foliar
sheath is densely covered with simple
to divided veins, mostly divided twice to
rarely thrice. The sheath margins are
irregular and entirely dentate, with small
and asymmetrical teeth.

5 Discussion

5.1 Taxonomic assignment and comparisons

The new equisetalean fossil from the
DCB, *Phyllothea douroensis* sp. nov.
(Fig. 3A), displays a large and well-
developed foliar sheath totally released
from the stem from the node (or distally
opened), cup-shaped, which are diagnostic
features of the fossil-genus *Phyllothea*
described by Brongniart (1828) (see
summary of the morphological characters
of the genus in Correia et al., 2021,
table 1; see also McLoughlin, 1992).

Among all known species of *Phyllothea*, *Phyllothea douroensis* sp. nov. is most similar to the Gondwanan *Phyllothea etheridgei* Arber, 1905 from the late Permian of Newcastle Series, New South Wales, Australia (Saksena, 1952, 1954; Boureau, 1964). Basal leaf whorls of *P. etheridgei* show a large and well-developed disc shaped foliar sheath with dentate margins (Fig. 4) and size comparable to that of *P. douroensis* sp. nov. However, they differ from the venation pattern in foliar sheaths. The veins of the foliar sheath of *P. douroensis* sp. nov. are divided at least twice to thrice (Fig. 3B), while veins of the foliar sheaths of *P. etheridgei* are simple, without any divisions (Fig. 4). Furthermore, there are some dissimilarities in the sheath margins of both species; *P. etheridgei* shows regular dentate margins, while the dentate margins of *P. douroensis* sp. nov. are relatively irregular or asymmetrical. The preservation state of the fossil material by compression can, however, have had some taphonomic influence on apparent asymmetrical shape of the foliar sheath of *P. douroensis* sp. nov. In addition, *P. douroensis* sp. nov. has similar foliar sheaths to those of the *Iberisetum* Correia et al., 2021, an endemic-like taxon from the Late Pennsylvanian of DCB, although they present structural differences especially in the shape of the foliar sheaths.

Only a single leaf whorl is described for the *P. douroensis* sp. nov., but based on its broad axis it is likely that it corresponds to a basal leaf whorl from a leafy axis with similar foliar polymorphism to that of *P. etheridgei* (Fig. 4).

5.2 Morphological similarity with the foliage of Gondwanan and Angaran floras and its palaeobiogeographical significance

The floras of the DCB are described as typical Euramerican floral elements. They were deposited and preserved in an intramontane environment within central tropical Pangaea in seasonal conditions during an interval of wet to dry

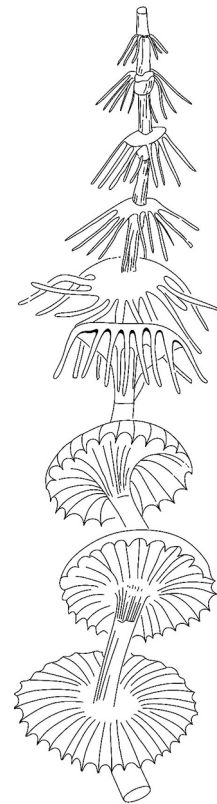


Figure 4. *Phyllothea* (*Raniganjia*?) *etheridgei* Arber, 1905 from the late Permian of Newcastle Series, New South Wales, Australia (Gondwana) showing foliar polymorphism. Reconstruction according to Saksena (1954; see Boureau, 1964, fig. 366).

climate transition in the Gzhelian (Late Pennsylvanian, ca. 304–299 Ma) (Correia & Murphy, 2020; Correia et al., 2016, 2018). These restricted environmental, climatic and ecological conditions led to origin to many plant forms with endemic morphological characteristics in this Euramerican region (e.g., *Lesleya iberiensis* Correia et al., 2016, *Acithea murphyi* Correia et al., 2018, *Douropteris alvarezii* Correia et al., 2019a, *Annularia noronhai* Correia et al., 2019b, *Annularia paisii* Correia et al., 2020, *Iberisetum wegneri* Correia et al., 2021). However, some unusual floral elements outside of the intramontane basin, such as the Gondwanan *Stellothea robusta* (Feistmantel) Surange & Prakash, have been documented in the lower Gzhelian strata of DCB (Correia et al., 2014a, 2018).

The new equisetalean fossil (Fig. 3A) from DCB described herein shows a strong morphological similarity with the *Phyllothea*-type foliage. The fossil-genus *Phyllothea* has an extensive geographic and stratigraphic range which has been globally recognized in upper Carboniferous–Early Cretaceous strata (e.g., Boureau, 1964). Several late Palaeozoic equisetaleans with *Phyllothea*-type foliage have been reported in both Gondwanan and Angaran provinces (e.g., Boureau, 1964; Meyen, 1971; Naugolnykh, 2002, 2004, Taylor et al., 2009; Elgorriaga et al., 2018). Rare Palaeozoic equisetalean records with endemic characteristics to Angaran floral province have also been occasionally reported in the upper Carboniferous of Iberian Massif (e.g., Broutin, 1974). For example, the first record of the Angaran endemic genus *Koretrophyllites* Radczenko outside of the Angara was documented by Broutin (1974) who described the *Koretrophyllites crassinervis* found in upper Gzhelian (Autunian–Stephanian, Upper Pennsylvanian) strata of the Guadalcanal Basin, Sevilla, in Spain. These occurrences suggest floral exchanges between Euramerica, Angara and Gondwana. Large-scale floral migrations have been documented among the different phyto-geographic provinces (e.g., Naugolnykh & Uranbileg, 2018). The presence of *Phyllothea* in DCB may indicate a distant migration of typical Gondwanan or Angaran floras to the Euramerican province. Such a possible scenario may mean that these floral migrations occurred when the different provinces shared similar climatic conditions for the same time intervals.

5.3 Systematic and evolutionary considerations

Once the type species (*Phyllothea australis*) comes from the Gondwanan floral province (e.g., Boureau, 1964, McLoughlin, 1992; McLoughlin et al., 2005; Srivastava & Agnihotri, 2010; Roesler & Iannuzzi, 2012), the attribution of the

new equisetalean fossil (*P. douroensis* sp. nov.) from DCB to the fossil-genus *Phyllothea* raises some questions from the systematic and evolutionary point view.

When Brongniart (1828) described *Phyllothea*, he established the fossil-family Phyllothecaceae (sensu lato) based on the vegetative parts attributed to this fossil-genus (Correia et al., 2021). Phyllothecaceae sensu lato comprises two families: Gondwanostachyaceae sensu stricto and Tchernoviaceae sensu stricto, two biologically and phyto-geographically distinct groups (e.g., Meyen, 1967, 1969; Coreia et al., 2021). The two families have very distinct reproductive structures but have similar foliage, i.e. *Phyllothea*-type (Meyen, 1967, 1969, 1971, 1987; Cúneo & Escapa, 2006; Weber, 2008; Srivastava & Agnihotri, 2010; Boardman & Iannuzzi, 2010). Since both groups arose in places with similar ecological conditions, this homoplasy (in the foliage) is due to convergent evolution (Meyen, 1967, 1987; Roesler & Iannuzzi, 2012; see also Naugolnykh, 2002). Foliage of *P. douroensis* sp. nov. is closely related to foliage of Phyllothecaceae sensu lato, but has no preserved reproductive organs that link either to Gondwanostachyaceae or to Tchernoviaceae.

The close resemblance to the endemic Australian *Phyllothea etheridgei* is very interesting, because it could indicate phylogenetic affinities between the Portuguese and Gondwanan species, i.e. with Gondwanostachyaceae. *P. etheridgei* has been renamed as *Raniganjia etheridgei* (Arber) Rigby, 1962a (De et al., 2003). *Raniganjia* Rigby, 1962b corresponds to a rare equisetalean member from the late Permian beds (Raniganj, Kamthi and Pachwara Formations) of Indian Gondwana, and equivalent Formations in Australia and Brazil (De et al., 2003). Later, McLoughlin (1992) considered *P. etheridgei* as an intermediate form in which leaves are variously fused or free, having pointed apices typical of *Phyllothea* but also showing transverse

striae characteristic of the genus *Raniganjia*. It is not possible to relate these intermediate forms to *P. douroensis* sp. nov. because only a single leaf whorl is described for the Portuguese species. However, it is very likely that *P. douroensis* sp. nov. corresponds to a convergent form of *Phyllothea*-type foliage to the Euramerican floral province.

6 Conclusions

In this work, we report the first occurrence of the equisetalean fossil-genus *Phyllothea*, named *Phyllothea douroensis* sp. nov., in the Portuguese Carboniferous and it is more an element of strong morphological convergence between distantly related floras. This new finding indicates that Phyllothecaceae sensu lato was not restricted only to Angaran and Gondwanan floral provinces, suggesting that late Palaeozoic equisetaleans with *Phyllothea*-type foliage occurred in Euramerican floral realm.

Acknowledgements

We thank to Museu da História Natural e da Ciência da Universidade do Porto (Portugal) for the laboratorial support. The authors also thank two anonymous reviewers for their useful comments on the submitted manuscript. This study was supported by Portuguese funds by Fundação para a Ciência e a Tecnologia, I.P. (Portugal) in the frame of the UIDB/00073/2020 and UIDP/00073/2020 projects of the I&D unit Geosciences Center (CGeo).

Author contributions

P.C. and C.B. wrote the manuscript. P.C. and A.A.S. prepared the figures. J.M. helped in the preparation of fossil sample and photographic documentation. P.C., C.B. and A.A.S. were involved in the taxonomic study of the new equisetalean fossil and corrected the text of manuscript. All authors discussed and approved the final manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

References

- AGARDH, C. H. (1825). *Aphorismi botanici. Classes plantarum, pars 1*. Berling, Lund.
- ARBER, E. A. N. (1905). *The Glossopteris flora*. British Universities Catalogue, London.
- ANDERSON, M. & ANDERSON, H. M. (1985). *Palaeoflora of southern Africa. Prodrum of southern African megaflores Devonian to Lower Cretaceous*. A.A. Balkema, Rotterdam.
- BERCHTOLD, F. W. & PRESL, J. S. (1820). *O přirozenosti rostlin*. Krause, Prague, Czech Republic.
- BOARDMAN, D. R. & IANNUZZI, R. (2010). Presence of the genus *Giridia*, sphenophyte, in the Paraná Basin (lower Permian, Rio Bonito Formation). *Revista Brasileira De Paleontologia*, 13(1), 5–12.
- BOARDMAN, D. R., IANNUZZI, R., & DUTRA, T. L. 2016. A new genus of Sphenopsida from the Lower Permian of the Paraná Basin, Southern Brazil. *Review of Palaeobotany and Palynology*, 233, 44–55.
- BOUREAU, E. (1964). *Traité de Paléobotanique III: Sphenophyta et Noeggerathiophyta*. Masson et Cie Éditeurs, Paris, France.
- BRONGNIART, A. T. (1828). *Prodrome d'une histoire des végétaux fossiles*. F. G. Levrault, Paris.
- BROUTIN, J. (1974). *Sur quelques plantes fossiles du Bassin Autuno-Stephanien de Guadalcanal (Province de Seville, Espagne)*. *Lagascalia*, 4(2), 221–237.
- COCKS, L. R. M. & TORSVIK, T. H. (2011). The palaeozoic geography of Laurentia and Western Laurussia: A stable craton with mobile margins. *Earth-Science Reviews*, 106(1–2), 1–51.
- CORREIA, P., MURPHY, J. B., SÁ, A. A., DOMINGOS, R. & FLORES, D. (2013). First Palaeozoic arachnid from Portugal and

- implications for Carboniferous palaeobiogeography. *Geological Journal*, 48, 101–107.
- CORREIA, P., ŠIMŮNEK, Z., PŠENIČKA, J., SÁ, A. A., DOMINGOS, R., CARNEIRO, A. & FLORES, D. (2014a). New paleobotanical data on the Portuguese Pennsylvanian (Douro Carboniferous Basin, NW Portugal). *Comunicações Geológicas*, 101, 409–414.
- CORREIA, P., NEL, A., SÁ, A. A., DOMINGOS, R., CARNEIRO, A. & FLORES, D. (2014b). A new Palaeodictyoptera from the Late Carboniferous of Portugal. *Annales de la Société Entomologique de France*, (n.s.), 49(4), 398–401.
- CORREIA, P., SÁ, A. A., MURPHY, J. B., ŠIMŮNEK, Z. & FLORES, D. (2016). *Lesleya* Lesquereux from the Pennsylvanian of the Iberian Massif: part of a dryland megaflora from the Variscan orogen, northwestern Portugal. *Canadian Journal of Earth Sciences*, 53, 883–895.
- CORREIA, P., ŠIMŮNEK, Z., SÁ, A. A. & FLORES, D. 2018. A new Late Pennsylvanian floral assemblage from the Douro Basin, Portugal. *Geological Journal*, 53, 2507–2531.
- CORREIA, P., ŠIMŮNEK, Z., CLEAL, C. J. & SÁ, A. A. (2019a). *Douropteris alvarezii* gen. nov., sp. nov., a new medullo-salean pteridosperm genus from the early Gzhelian (Late Pennsylvanian) of Douro Basin (NW Portugal). *Geological Journal*, 54, (3), 1567–1577.
- CORREIA, P., ŠIMŮNEK, Z., CLEAL, C. J., VALLOIS, B., DOMINGOS, R. & SÁ, A. A. (2019b). On a new species of the calamitalean fossil-genus *Annularia* from the Douro Basin (lower Gzhelian; NW Portugal). *Historical Biology*, 33 (2), 258–267.
- CORREIA, P., BASHFORTH, A. R., ŠIMŮNEK, Z., CLEAL, C. J., SÁ, A. A. & LABANDEIRA, C. C. (2020). The history of herbivory on sphenophytes: a new calamitalean with an insect gall from the Upper Pennsylvanian of Portugal and a review of arthropod herbivory on an ancient lineage. *International Journal of Plant Sciences*, 181, 387–418.
- CORREIA, P. & MURPHY, J. B. (2020). Iberian-Appalachian connection is the missing link between Gondwana and Laurasia that confirms a Wegenerian Pangaea configuration. *Scientific Reports*, 10(1), 2498.
- CORREIA, P., ŠIMŮNEK, Z. & SÁ, A. A. (2021). The equisetalean *Iberisetum wegneri* gen. nov., sp. nov. from the Upper Pennsylvanian of Portugal. *Historical Biology*. <https://doi.org/10.1080/08912963.2021.1874373>
- CÚNEO, R. & ESCAPA, I. (2006). The Equisetalean genus *Cruciaetheca* nov. from the Lower Permian of Patagonia, Argentina. *International Journal of Plant Sciences*, 167(1), 167–177.
- DE, A., DE, B., BERA, S. (2003). First record of *Raniganjia bengalensis* (Rigby) Pant & Nautiyal from lower Permian beds (Barakar Formation) of South Karanpura coalfield, Jharkhand, India. *Journal of the Geological Society of India*, 61, 487–490.
- DOMINGOS, L. C. G., FREIRE, J. L. S., GOMES DA SILVA, F., GONÇALVES, F., PEREIRA, E., RIBEIRO, A. (1983). The structure of the intramontane Upper Carboniferous basins in Portugal. In: Lemos de Sousa, M. J. & Oliveira, J. T. (Eds). *The Carboniferous of Portugal. Memórias dos Serviços Geológicos de Portugal* (Lisboa) 29; pp. 187–194.
- EAGAR, R. M. C. (1983). The non-marine bivalve fauna of the Stephanian C of the North Portugal. In: Lemos de Sousa, M. J. & Oliveira, J. T. (Eds). *The Carboniferous of the Portugal. Memórias dos Serviços Geológicos de Portugal* (Lisboa) 29; pp. 179–185.
- ELGORRIAGA, A., ESCAPA, I. H., ROTHWELL, G. W., TOMESCU, A. M. F. & CÚNEO, N. R. (2018). Origin of Equisetum: evolution of horsetails (Equisetales) within the major euphyllophyte clade Sphenopsida. *American Journal of Botany*, 105(8), 1286–1303.
- LEMONS DE SOUSA, M. J. & WAGNER, R. H. (1983). General description of the terrestrial Carboniferous basins in Portugal and history of investigations. In: Lemos de Sousa, M. J. & Oliveira, J. T. (Eds). *The Carboniferous of Portugal. Memórias dos Serviços Geológicos de Portugal* (Lisboa) 29; pp. 117–126.

- LOUREIRO, J. P., CORREIA, P., NEL, A. & PINTO DE JESUS, A. (2010). *Lusitaneura covensis* nov. gen. & nov. sp., first Caloneuroidea from the Carboniferous of Portugal (Insecta: Pterygota: Panorthoptera). *Annales de la Société Entomologique de France*, (n.s.), 46(1-2), 242-246.
- MAHESHWARI, H. K. (1974). Palaeozoic Lycopsida and Sphenopsida. In: Sumngr, K. R., Whanpal, R. N. & Bharadwa, D. C. editors. *Aspects and appraisal of Indian palaeobotany*. Birbal Sahni Institute of Palaeobotany, Lucknow, p. 51-61.
- MCCLOUGHLIN, S. (1992). Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 1. *Palaeontographica Abteilung B*, 228, 105-149.
- MCCLOUGHLIN, S., LARSSON, K. & LINDSTRÖM, S. (2005). Permian plant macrofossils from Fossilryggen, Vestfjella, Dronning Maud Land. *Antarctic Science*, 17, 73-86.
- MEYEN, S. V. (1967). New data on the relationship between Angara and Gondwana late Paleozoic floras. Gondwana Stratigraphy, IUGS 1st Gondwana Symposium, Buenos Aires 1967, *UNESCO Earth Sciences* 2, p. 144-152.
- MEYEN, S. V. (1969). The Angara members of the Gondwana genus *Barakaria* and its systematical position. *Argumenta Palaeobotanica*, 3, 1-14.
- MEYEN, S. V. (1971). *Phyllothea*-like plants from the Upper Palaeozoic flora of Angaraland. *Palaeontographica B*, 133, 1-33.
- MEYEN, S. V. (1982). The Carboniferous and Permian floras of Angaraland (A synthesis). *Biological Memoirs*, 7, 1-110.
- MEYEN, S. V. (1987). *Fundamentals of Palaeobotany*. Chapman & Hall, New York, USA.
- NAUGOLNYKH, S. V. (2002). *Paracalamitina striata* — a newly reconstructed equisetophyte from the Permian of Angaraland. *Journal of Paleontology*, 76(2), 377-385.
- NAUGOLNYKH, S. V. & URANBILEG, L. (2018). A new discovery of *Glossopteris* in southeastern Mongolia as an argument for distant migration of Gondwanan plants. *Journal of Asian Earth Sciences*, 154, 142-148.
- OSHURKOVA, M. V. (1996). Paleoeological parallelism between the Angaran and Euramerican phytogeographic provinces. *Review of Palaeobotany and Palynology*, 90, 99-111.
- PFEFFERKORN, H. W. & WANG, J. (2016). Paleoeology of Noeggerathiales, an enigmatic, extinct plant group of Carboniferous and Permian times. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 448, 141-150.
- PINTO DE JESUS, A. (2001). *Génese e Evolução da Bacia Carbonífera do Douro (Estefaniano C inferior, NW de Portugal); Um Modelo* [unpublished Ph.D. dissertation]. University of Porto, Portugal.
- PINTO DE JESUS, A. (2003). Evolução sedimentar e tectónica da Bacia Carbonífera do Douro (Estefaniano C inferior, NW de Portugal). *Caderno Lab Xeolóxico Laxe Coruña*, 28, 107-125.
- PREVEC, R., GASTALDO, R. A., NEVELING, J., SAMUEL, B. R. & LOOY, C. V. (2010). An autochthonous glossopterid flora with latest Permian palynomorphs and its depositional setting in the Dicynodon Assemblage Zone of the southern Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 292, 391-408.
- RIGBY, J. F. (1962a). On a collection of plants of Permian age from Baralaba, Queensland. *Proceedings of the Linnean Society of New South Wales*, 87(3), 341-351.
- RIGBY, J. F. (1962b). The taxonomic position of *Actinopteris indica* Srivastava. *Proceedings of the Linnean Society of New South Wales*, 86(3), 299-304.
- ROESLER, G. A. & IANNUZZI, R. (2012). Nova espécie de Sphenophyta no Eopermiano do Rio Grande do Sul (Grupo Itararé, Bacia do Paraná). *Revista Brasileira de Paleontologia*, 15, 141-152.
- SAKSENA, S. (1952). On a new species of *Phyllothea* (P. Sahnii) from the South Rewah Gondwana basin, Central India,

- and its comparison with *P. Etheridgei* from the New Castle Series, New South Wales, Australia. *The Palaeobotanist*, 1, 409–415.
- SAKSENA, S. (1954). Reconstruction of the vegetative branches of *Phyllothea etheridgei* Arber and *P. Sahnii* Sakse-
na. *Palaeobotanist*, 3, 51–53.
- SHUTE, C. H. & CLEAL, C. J. (1996). Palaeobotany in museums. *Geological Curator*, 4, 553–559.
- SRIVASTAVA, A. K. & AGNIHOTRI, D. (2010). Dilemma of late Palaeozoic mixed floras in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 298, 54–69.
- SUNDERLIN, D. (2010). Evidence for a western extension of the Angaran phytogeographic province in the Early Permian. *International Journal of Coal Geology*, 83, 266–275.
- TAYLOR, T. N., TAYLOR, E. L. & KRINGS, M. (2009). *Paleobotany: The biology and evolution of fossil plants*. Amsterdam, Academic Press.
- TOWNROW, J. A. (1955). On some species of *Phyllothea*. *Journal and Proceedings of the Royal Society of New South Wales*, 83, 39–63.
- VAL, G. B. (2003). Development of the palaeogeography of Pangaea from Late Carboniferous to Early Permian. *Palaeogeography, Palaeoclimatology, Palaeoecology* 196, 125–155.
- VERBITSKAYA, N. G. & RADCHENKO, G. P. (1968). New Siberian arthropods. In: Zanina, I. E., Kiparisova, L. D., Markovsky, B. P., Lokrovskiy, I. M., Miklouho-Maclay, K. V. & Radchenko, G. P. (Eds). *New species of ancient plants and invertebrates of the USSR*. Publishing House Nedra, Moscow, Russia [in Russian]; pp. 13–18.
- WAGNER, R. H. (1983). The palaeogeographical and age relationships of the Portuguese Carboniferous floras with those of other parts of the Western Iberian Peninsula. In: Lemos de Sousa, M. J. & Oliveira, J. T. (Eds). *The Carboniferous of Portugal. Memórias dos Serviços Geológicos de Portugal*. Lisboa, 29; pp. 153–177.
- WAGNER, R. H. (2004). Climatic changes as mirrored by Carboniferous and Permian floral distributions. *Monografías del Jardín Botánico de Córdoba*, 39, 29–39.
- WAGNER, R. H. & LEMOS DE SOUSA, M. J. (1983). The Carboniferous Megafloras of Portugal – A revision of identifications and discussion of stratigraphic ages. In: Lemos de Sousa, M. J. & Oliveira, J. T. (Eds). *The Carboniferous of Portugal. Memórias dos Serviços Geológicos de Portugal* (Lisboa) 29; pp. 127–152.
- WEBER, R. (2008). Homomorfismo en Equisetaceae del Triásico: *Asinisetum* gen. nov., *Equisetites aequecaliginosus* Weber y conos asociados de Sonora, México. In: Weber, R. (Ed). *Plantas triásicas y jurásicas de México* (Vol. 115). Boletín: Universidad Nacional Autónoma de México, Instituto de Geología; pp. 1–83.



Publisher's note: Eurasia Academic Publishing Group (EAPG) remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access: This article is licensed under a Creative Commons Attribution-NonCommercial 4.0 International (CC BY-NC 4.0) licence, which permits copy and redistribute the material in any medium or format for any purpose, even commercially. The licensor cannot revoke these freedoms as long as you follow the licence terms. Under the following terms you must give appropriate credit, provide a link to the license, and indicate if changes were made. You may do so in any reasonable manner, but not in any way that suggests the licensor endorsed you or your use. If you remix, transform, or build upon the material, you may not distribute the modified material.

To view a copy of this license, visit <https://creativecommons.org/licenses/by-nc/4.0/>.