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First record of Late Miocene *Dendrophyllia* de Blainville, 1830 (Scleractinia: Dendrophylliidae) in Taiwan

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ABSTRACT

The recently exposed outcrops along the Dahan River in Shulin, northern Taiwan revealed diverse and abundant marine fossils including molluscs, shark and ray teeth, sand dollars, and otoliths from a wide range of fish taxa. In addition, numerous small and fragile fossil scleractinians were found and identified here as *Dendrophyllia* sp., from the mainly azooxanthellate (90%) dendrophylliid family. Lithology of the outcrops are mainly composed of grey sandstones from the Tapu Formation (Late Miocene), overlying on a layer of basaltic tuff. The absolute age of the boundary between the Tapu Formation and the underlying Nanchuang Formation is 8 Ma, which provides indications on the maximum age possible for the scleractinian fossils found in this study. Back then, the marine ecosystem in which the sampled *Dendropyllia* specimens grew was probably a turbid shallow coastal environment with muddy to sandy bottom, likely at the vicinity of a river estuary, as suggested by the combined presence of previously reported fish otoliths. To our knowledge, this is the first record of *Dendrophyllia* fossils from Taiwan.

1. INTRODUCTION

Over the last decades, coral reefs have been impacted by significant degradations from the ongoing anthropogenically-caused climate change and the increasing local human pressures that jeopardize the ability of coral reefs to persist in the near future (Hughes et al. 2017). These predictions are contrasted by the fact that coral reef ecosystems have existed for more than 500 million years (Riegl et al. 2009). The appearance of modern coral (Scleractinia) can be traced back to at least the Permo-Triassic mass-extinction event (251 Ma) when they gradually became the major contributors to reef accretion (Pandolfi 2011). Since then, scleractinian corals have survived two additional mass-extinction events (the Triassic-Jurassic event at 200 Ma and the Cretaceous-Paleogene event at 66 Ma), which were triggered by cataclysms (massive volcanic activities for the Triassic-Jurassic and the Cretaceous-Paleogene events; and an asteroid impact for the Cretaceous-Paleogene event) that drove atmospheric CO_2 levels above 3000 ppmv (Retallack 2002). Current studies have suggested that our planet, and especially coral reef ecosystems are currently in the midst of another mass-extinction event, driven by the intensive anthropogenic pressures at planetary scale (Pandolfi et al. 2011).

The fossil reefs, and the calcified remains within, are unique witnesses of the past, holding critical physical, biological and chemical information (Hubbard 2011). Studying these remains, in particular coral fossils, allows scientists to reconstruct the functioning of the coral ecosystems prior to any anthropogenic exploitation or under different climatic contexts that are nowadays no longer observable (Pandolfi 2011). Paleoecological studies can further unveil the geological legacies on reefs' resilience abilities through their respective long-term evolutionary trajectory that led to the more or less diverse local scleractinian coral communities (Huang et al. 2015). These past pieces of knowledge are critically needed by the scientific community in order to adequately preserve reef functioning and ultimately ensure the survival of this essential ecosystem (Cybulski et al. 2020).

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Taiwanese coral reefs and non-reefal coral communities are among the most diverse marine ecosystems on earth, hosting over a third of the world scleractinian diversity (558 species, Dai and Cheng 2020) and over 1400 reef fish species (Denis et al. 2019a). The extraordinary biodiversity hosted by Taiwanese reefs, along with the coastal protection and recreational activities offered by this ecosystem, constitute a critical economic resource to the Taiwanese economy, with an average value of 514.417 US$/km^2/year (Spalding et al. 2017). However, the multiple anthropogenic pressures along with the highly active typhoon regime and recurrent heat stress anomalies have induced major degradations of the Taiwanese reefs (Kuo et al. 2012; Ribas-Deulofeu et al. 2016, 2021; Denis et al. 2019b; Keshavmurthy et al. 2019), making them one of the five most threatened reef regions in South-East Asia (Burke et al. 2002). While modern Taiwanese reef biota have been relatively well characterized, little is known of their past long-term evolutionary trajectory which led to the diversification of its highly diverse scleractinian coral communities (Huang et al. 2015). In the 1980-90s, research papers have reported free-living coral fossils from the Plio-Pleistocene deposits in Miaoli, Tainan and Hengchung Peninsula along with a few *Cyphastrea* sp., *Coscinera exesa*, and dendrophyllid fossils (*Balanophyllia oulangiformis*, *Heteropsammia ovalis* and *michelini* and, *Leptopsammia formosa* previously reported as a *Balanophyllia*) (Hu and Tao 1982; Hu 1987a, b, 1988, 1990). In addition, Pleistocene coral fossils have been found in Takangshan area, near Kaoshiung City (Wang et al. 2006). In this study, a wide variety of scleractinian fossils was reported, including free-living corals such as *Cycloseris*, *Fungia*, *Heliofungia*, and *Herpolitha* (Wang et al. 2006). The fossil scleractinian community in the study of Wang et al. (2006) was also composed of specimens of *Acropora*, *Acanthastrea*, *Cyphastrea*, *Dipsastreae*, *Favites*, *Goniopora*, *Goniastrea*, *Galaxea*, *Pachyseris*, *Porites*, and *Turbinaria*, which was the only representative of the dendrophylliids (Wang et al. 2006). More diverse scleractinian communities have been reported from uplifted Holocene terraces in Ludao and Lanyu (Inoue et al. 2011; Ota et al. 2015; Shen et al. 2018). The fossil specimens presented in our study constitutes the first report of Late Miocene scleractinian fossils from Shulin area, northern Taiwan, which hold environmental and ecological information that inform us on the formation of the Taiwanese scleractinian community at a much earlier time than the previous studies in the country on the scleractinian fossils (Hu and Tao 1982; Hu 1987a, b, 1988, 1990; Wang 1997; Yamaguchi and Ota 2004; Wang et al. 2006; Inoue et al. 2011; Ota et al. 2015; Shen et al. 2018).

2. MATERIALS AND METHODS

2.1 Study Area and Geological Setting

Fossil specimens were sampled in two sites, SL-3 and SL-4 (Fig. 1, Supplementary Fig. S1), along the Dahan River in Shulin District, New Taipei City (Fig. 1). In the sampling area, the boundary between the Nanchuang Formation and overlying Tapu Formation are exposed (Lin et al. 2021), and the fossils were collected from the lowest part of the Late Miocene Tapu Formation (Fig. 2). In the outcrop, a notable basaltic tuff layer of approximately two meters can be observed. The absolute age of the boundary between the Tapu Formation and the underlying Nanchuang Formation is 8 Ma (Tsao et al. 1992), which provide indications on the maximum age possible for the scleractinian fossils found in this study. The difference in the sandstones seen at SL-4 (24°57'32.82"N, 121°22'50.75"E, Fig. 1c) and SL-3 (24°57'40.25"N, 121°23'05.18"E) is that the one observed in SL-3 is disrupted by a layer of matrix-supported tuff conglomerates about 40 cm thick (Fig. 1d). The bed attitude of those exposed sandstone strata at both sites have a strike of N50°E and a dip of 80° toward the west. According to sedimentological studies (Ho 1986; Hong and Wang 1988), the Tapu Formation is composed of inshore deposits.

2.2 Sampling

Fossils from Shulin area were first reported in 2010 (Lin 2010) but the site reported therein was flushed away in the rainy seasons between 2015 to 2016. Our coral specimens, sampled from new outcrops at sites SL-3 and SL-4 (Figs. 1 and 2, Supplementary Fig. S1), can be frequently observed on the surface of the strata (Lin et al. 2021; Lin and Chien 2022). However, fragility of coral specimens required delicate sampling using hammer and chisel. Specimens were then cleaned using water and a toothbrush to remove the sediments.

3. RESULTS

During the investigations of the Shulin sites, diverse and abundant marine remains have been found, including molluscs, shark and ray teeth, sand dollars, and > 1700 otoliths (from > 30 otolith-based taxa) (Lin and Chien 2022). In addition, numerous small fragments of scleractinians were found (Fig. 3). However, all these fragments likely belong to a single species of the genus *Dendrophyllia*. Fewer specimens (< 20) were found in SL-3 than in SL-4 and most of them could not be extracted from their surrounding sediment material without breaking the specimens. *Dendrophyllia* specimens in SL-4 were easily found and relatively abundant but extremely fragile, likely due to subaerial weathering and rainwater leaching (Lin and Chien 2022). The collected specimens in SL-4 rarely exceeded 5 cm in size and were mostly found as 1 to 2 cm fragments (Fig. 3). Many were broken during extraction and simple ultrasonic washing was sufficient to break them further.

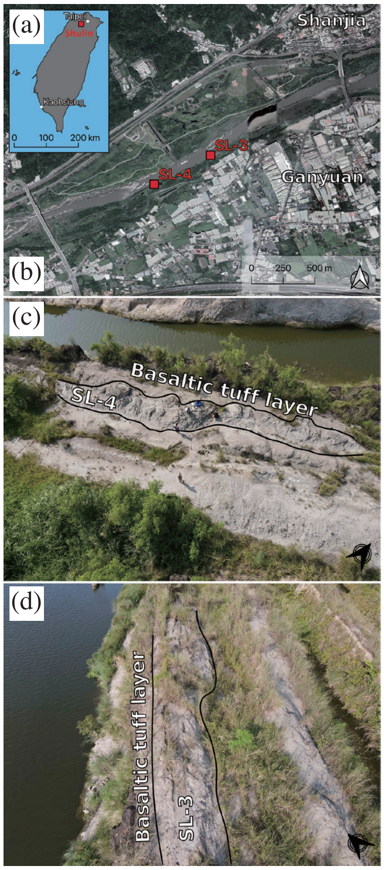

Fig. 1. Study sites. (a) Location of Shulin District, New Taipei City. (b) Sampled sites SL-3 and SL-4 along the Dahan River, in Shulin area. (c) Aerial view of SL-4 and, (d) Aerial view of SL-3.

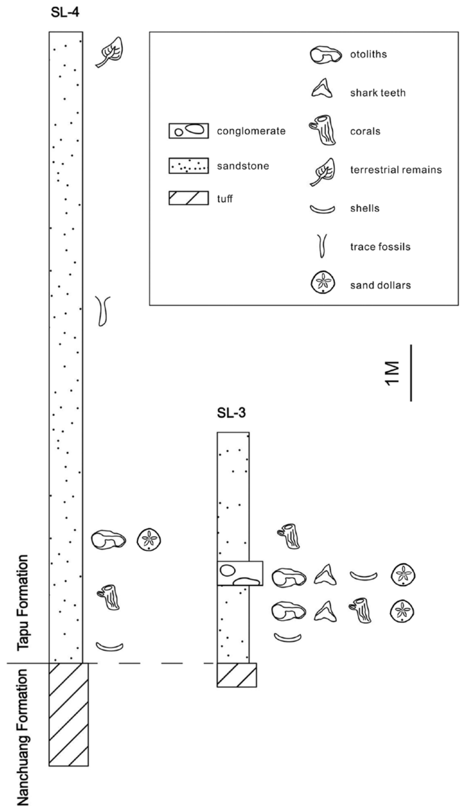

Fig. 2. Stratigraphic columns of the studied sites (modified after Lin and Chien 2022).

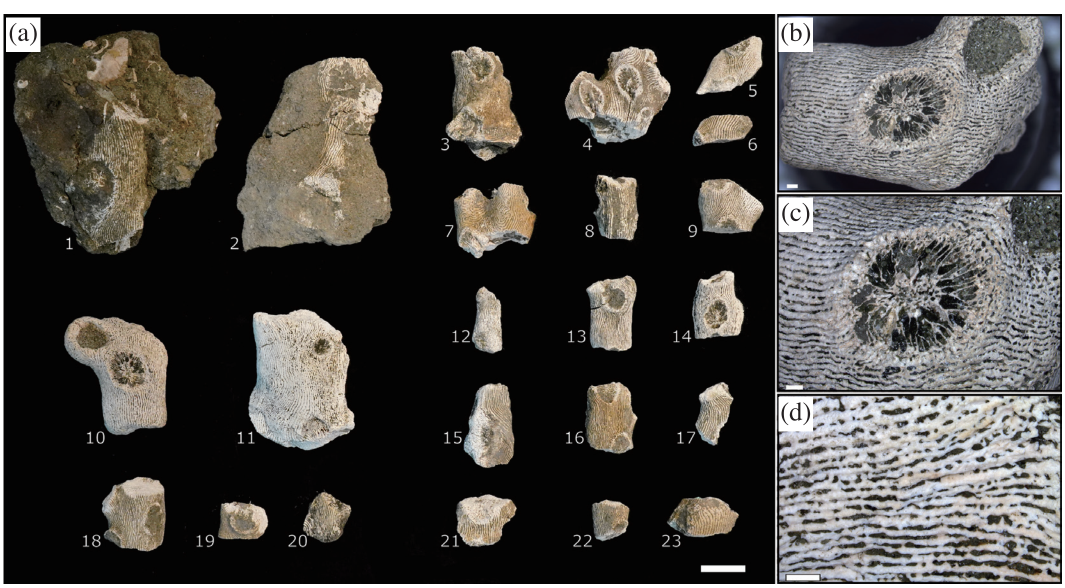

Fig. 3. *Dendrophyllia* sp. fossils from SL-4. (a) General view of 23 fossil specimens deposited at the Biodiversity Research Museum, Academia Sinica, Taiwan (BRMAS, http://museum.biodiv.tw/eng). (Museum references: 1. *ASIZF0100142*, 2. *ASIZF0100148*, 3. *ASIZF0100149*, 4. *ASIZF0100150*, 5. *ASIZF0100151*, 6. *ASIZF0100159*, 7. *ASIZF0100152*, 8. *ASIZF0100153*, 9. *ASIZF0100154*, 10. *ASIZF0100143*, 11. *ASIZF0100144*, 12. *ASIZF0100145*, 13. *ASIZF0100146*, 14. *ASIZF0100147*, 15. *ASIZF0100155*, 16. *ASIZF0100157*, 17. *ASIZF0100158*, 18. *ASIZF0100156*, 19. *ASIZF0100160*, 20. *ASIZF0100161*, 21. *ASIZF0100162*, 22. *ASIZF0100163*, 23. *ASIZF0100164*) (b) Close-up view of specimen *ASIZF0100143*. (c) Close-up view of the corallite of specimen *ASIZF0100143*, showing a Pourtalès arrangement of the septa. (d) Close-up view of the costae of specimen *ASIZF0100144*. Scale bar in figure (a) is 1 cm while in (b), (c), and (d), the scale bars represent 1 mm.

3.1 Systematic Paleontology

Class: Anthozoa Ehrenberg, 1834
Order: Scleractinia Bourne, 1900
Suborder: Dendrophylliina Vaughan and Wells, 1943
Family: Dendrophylliidae Gray, 1847
Genus: *Dendrophyllia* de Blainville, 1830
Type species: *Dendrophyllia ramea* (Linnaeus, 1758)
Diversity: A total of 85 species of *Dendrophyllia* were listed by Cairns (2001), including 29 valid extant species and 56 extinct species, among which two *nomina nuda* species (one extant and one extinct species). The oldest *Dendrophyllia* was reported from the Campanian-Maastrichtian (Late Cretaceous) of Tibet (Löser and Liao 2001).
Specimen description: Dendroid colonies. Septa display a four-cycle arrangement and are organized in Pourtalès plan (Fig. 3). Columella is porous with a circular or elliptical shape (Fig. 3). Budding is extratentacular. The costae are well-defined with deep interstices presenting irregular connections between costae (Fig. 3, Supplementary File S1). Despite superficial erosion of the costae, they occasionally seem to display granular or even hispid aspects (Fig. 3). From the specimens on which corallites and/or branch diameters were measurables, 20 specimens were randomly picked for measurements. Mean corallites diameter is 6.15 ± 1.38 mm, with a minimum of 4.58 mm and a maximum of 8.87 mm, while mean branch diameter is 9.77 ± 4.43 mm with branch diameters ranging from 4.39 to 21.54 mm.
Remarks: *Dendrophyllia* colonies originate from a single basal stem and have been organized into three groups by Cairns (2001):
- Group 1: arborescent colonies with axial corallites (e.g., *D. ramea*, *D. cribosa*),
- Group 2: small, bushy colonies with sparse branches from the main stem (e.g., *D. carleenae*, *D. cornigera*),
- Group 3: dendroid colonies with sympodial branching (e.g., *D. minima*, *D. oldroydae*).

Specimens presented in this study belong to the Group 2, but due to the preservation condition, we are not able to identify them to species level.
Structure from Motion (SfM) 3D model of the specimen ASIZF0100147 is provided in the supplementary materials (Supplementary File S1).
Locality and Horizon: Shulin, basal Tapu Formation
Museum access numbers: Biodiversity Research Museum, Academia Sinica, Taiwan (BRMAS, http://museum.biodiv.tw/eng), Specimens ASIZF0100142 to ASIZF0100164.

4. DISCUSSION

4.1 Taxonomy and Ecology of Modern *Dendrophyllia*

Collected specimens in SL-3 and SL-4 have been identified as a Cairns' Group 2 type of *Dendrophyllia* sp. (Fig. 3, Supplementary File S1). Dendrophylliids are at 90% azooxanthellate (~149 out of 166 modern species, Cairns 2001), which has allowed them to colonize a wide geographic and bathymetric range, including cryptic locations or caves. Indeed, in the 21st century, living colonies of modern dendrophylliids are found from the North Sea to the sub-Antarctic region, at depths ranging from 0 to 2165 m (Cairns 2001). *Dendrophyllia* are among the azooxanthellate genera of the dendrophylliids and colonize seafloors up to 900 m in depth (Hoeksema and Cairns 2021). To date, 85 species of *Dendrophyllia* have been described, including 56 extinct species (Cairns 2001). An additional 72 species names have been identified as either synonymy or former *Dendrophyllia* species that have now been renamed and attributed to other dendrophylliids, mainly *Tubastraea*, *Eguchipsammia*, and *Enallopsammia* (Hoeksema and Cairns 2021).

In Taiwan, modern scleractinian diversity (558 species) accounts for two species of *Dendrophyllia* [*D. alcocki* (Wells 1954) and *D. arbuscula* (Van der Horst 1922)] along with 29 other species of dendrophylliids from the genera *Balanophyllia* (8 species), *Turbinaria* (7 species), *Tubastraea* (6 species), *Eguchipsammia* (4 species.), *Cladopsammia* (1 species), *Enallopsammia* (1 species), *Endopachys* (1 species), and *Heteropsammia* (1 species) (Dai and Cheng 2020). *D. arbuscula* (Van der Horst 1922) has been reported on hard substrates in Taiwan at depths from 45 to 240 m, while *D. alcocki* (Wells 1954) are found from 118 to 570 m (Dai and Cheng 2020). In addition, an early underwater survey of the marine biological diversity of the Southern Taiwan (Kenting) has reported three unidentified species of *Dendrophilla*, observed as dominant coral species along *Tubastrea aurea* in shallower depths (5 to 20 m) where walls, blocks and boulders created habitats with reduced light (Jones et al. 1972).

4.2 Field Taphonomy Observations

Although the *Dendrophyllia* skeletons retrieved no longer present the rough sandy aspect that characterize them, these fossil corals are considered well preserved (Fig. 3). Based on field observations, the bioclasts in sandstones were deposited as matrix-supported, and no firm substrate for *Dendrophyllia* growth was found in the sandstone at the two locations (Figs. 1c, d, and Supplementary Fig. S1). Therefore, these sandstone strata and tuff conglomerate appear to be mass-transported deposits, and the fossil corals may not be buried *in situ* but reflecting a concentration of geological events.

4.3 Paleo-Ecological Implications from Fossil Assemblages

The marine ecosystem that constituted SL-3 and SL-4 were probably not as deep as we could have expected it to be from the presence of *Dendrophyllia* spp. (depths ranging from ~40 to 600 m for extant species) but was a turbid shallow coastal environment with muddy to sandy bottom, likely at the vicinity of a river estuary. Indeed, coastal marine ecosystems at the proximity of river mouths usually present turbid conditions, which would be consistent with the presence of azooxanthellate corals such as *Dendrophyllia* sp.; as turbidity reduces the light penetration in the water column. This is reinforced by the sedimentary environment of the Tapu Formation as well as by the presence of sand dollars but most of all, by the numerous Ariidae and Sciaenidae otoliths retrieved in these sites by Lin and Chien (2022).

4.4 Fossil Records of *Dendrophyllia*

To date, the oldest dendrophylliid geological record can be dated back to the Late Pliensbachian (Early Jurassic), from Slovenia (Turnšek et al. 2003). Whilst, the oldest *Dendrophyllia* record is from the Campanian-Maastrichtian (Late Cretaceous), from the Tibetan region by Löser and Liao (2001). Fossil specimens of *Dendrophyllia* have been found from a wide range both in time and space (Table 1). Combining data from Cairns (2001), the Paleobiological Database (https://www.paleobiodb.org/classic) and our knowledge, specimens from this study are the first fossil *Dendrophyllia* recorded from Taiwan.

Table 1. Locations and geological epochs of recorded fossils of *Dendrophyllia* spp.: (a) in Cairns (2001) and (b) on the Paleobiology database (https://www.paleobiodb.org/classic). The * represents fossils recorded in the present study.

		Cretaceous	**Paleogene**			**Neogene**		**Quaternary**
		Late Cretaceous	**Paleocene**	**Eocene**	**Oligocene**	**Miocene**	**Pliocene**	**Pleistocene**
Asia	China	b						
	Japan					a, b		a
	Taiwan					*		
South-East Asia	Borneo						a	
	Indonesia						b	b
	Java					a	a	
	Myanmar				b	a		
South Pacific	Australia					b		
	New Zealand		b	a, b		b		
	Tasmania					a		
	Vanuatu							a, b
USA	Alabama		b	a, b				
	California			a, b	b		a, b	
	Louisiana			a, b				
	Mississippi			b				
	South Carolina			a				
	Washington			a, b	a, b			
Caribbean	Dominican Republic					b	b	
	Grenada					b		
	Jamaica	b						
South America	Brazil					b		
	Peru			a, b				
	Venezuela				a, b	b		
Europe	Austria				a			
	Crete					a		
	Czech Republic					b		
	Czechoslovakia (Former)					a		
	Denmark		a, b					
	England			a				

Table 1. (Continued)

		Cretaceous	Paleogene			Neogene		Quaternary
		Late Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene
Europe	France				b	a, b		
	Germany					b		
	Greece							b
	Greenland		a, b					
	Italy		b	a	a	a, b	a, b	b
	Netherlands	b						
	Poland					a, b		
	Portugal					b		
	Romania					b		
	Slovakia		b	b				
	Slovenia		b	b				
	Spain		b	a		b		
	Sweden		a, b					
	Ukraine		b	b				
Russia	Russia		b					
Middle-East	Iran					b		
	United Arab Emirates	b						
Africa	Egypt		b			a, b		
	Morocco					b		
	Somalia		b		a, b	b		

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