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Qualitative and quantitative analyses of Middle Eocene odontaspidid shark (*Brachycarcharias*) from Wadi Garawi area, north Eastern Desert, Egypt

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Abstract

The present study performs various analyses on the fossil shark teeth qualitatively and quantitatively. Fifty-eight fossil teeth were collected from the Middle Eocene deposits exposed at Wadi Garawi area, north Eastern Desert, Egypt. This succession is represented by the Guishi Member of the Observatory Formation, consisting mainly of limestones rich in shark teeth, with fossiliferous marls and sandstone interbeds. Through qualitative analysis, the collected teeth were assigned to three Brachycarcharias species; B. atlasi (Arambourg), B. lerichei (Casier), and B. twiggsensis (Case). In order to discriminate among the different Brachycarcharias species, the ImageJ and MorphoJ software packages were utilized to perform various morphometric analyses, including configuration of distinct landmarks, procrustes superimposition analysis, principal component analysis, and thin plate spline deformation plots. Besides these quantitative analyses, careful qualitative examination highlights considerable variations among the different Brachycarcharias species. In addition, these analyses support that the species Brachycarcharias twiggsensis (Case) can be attributed to a different genus, Tethylamna Cappetta and Case 2016.

1. Introduction

The Eocene exposures represent about 21% of the surface area of Egypt with varied lithologies[1, 2, 3, 4]. The Middle-Late Eocene exposures are prominent in the mountainous blocks around Cairo-Suez Road in north Eastern Desert [3, 5]. At Wadi Garawi area, the Middle Eocene deposits are represented by the Guishi Member of the Observatory Formation (Fig.1) [6]. These Eocene exposures were treated intensively from stratigraphical and paleontological aspects [5, 7, 8, 9, 10, 11, 12, 13]. However, the included shark teeth have not been reported so far. Sand tiger sharks are extant selachians including the family Odontaspididae (order: Lamniformes), distributed across tropical to cold-waters regions, occupying habitats from continental shelf zones to upper and lower continental slopes [14, 15, 16, 17]. The extinct sand tiger shark *Brachycarcharias* Cappetta and Nolf [17]shows a worldwide distribution across the northern and southern hemispheres during the Early Paleogene, reaching its maximum geographic distribution during the Middle Eocene [18, 19, 20].

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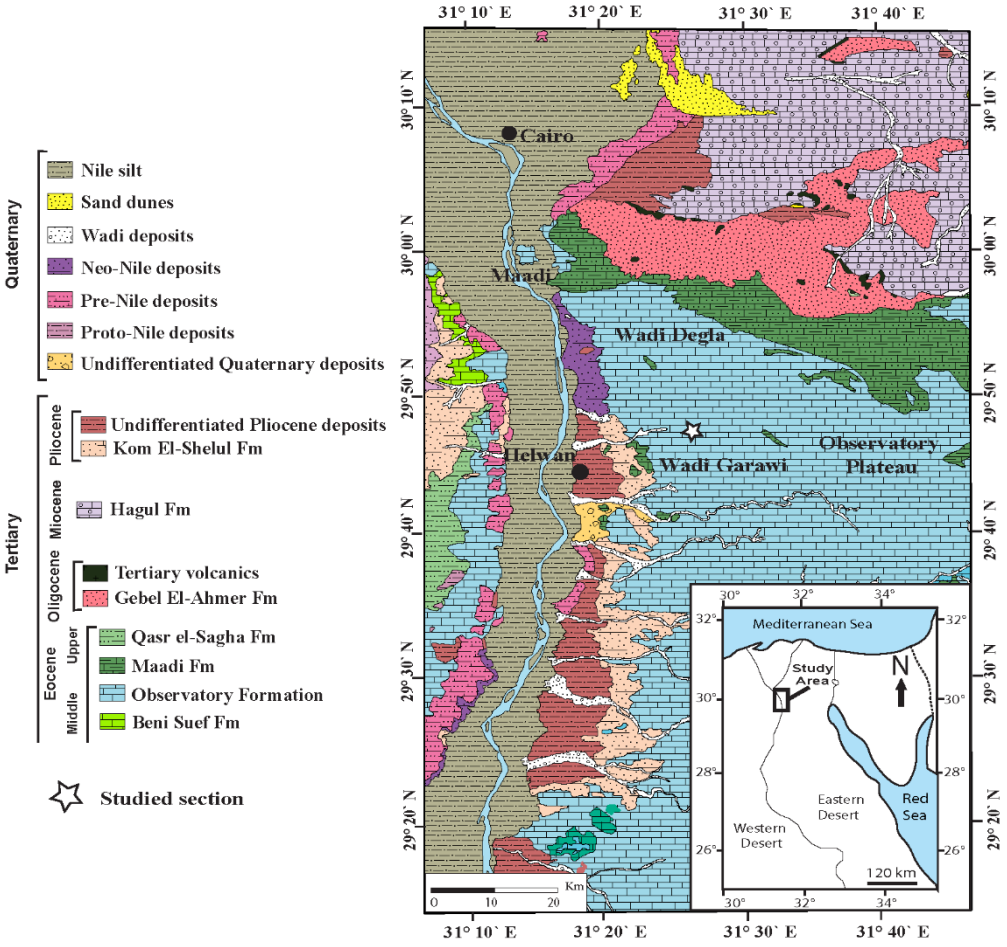

Fig.1. Location map and geological map of the study area, modified after Abd El-Gaied et al. [5]

Cappetta and Case [21]questioned the validity of *Brachycarcharias twiggsensis* [22], and assigned this species to a genus reported from the Lutetian deposits of Alabama, the *Tethylamna*.

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Species-level identification of fossil sharks was based solely on the qualitative morphological characteristics of the isolated teeth, with no technique for quantitative reassessment. In the present study, a qualitative study is used to identify the different teeth specimens, and a quantitative technique is also applied to assess the species discrimination. The morphometric analysis is considered a prominent technique to assess and interpret the shape variations of the different shark species through utilizing landmark coordinate points to capture the shape [23, 24, 25, 26, 27].

The objectives of the present work are: (1) to utilize the qualitative features of the different teeth specimens recovered from Wadi Garawi area, north Eastern Desert, Egypt, for species-level identification; (2) to perform various quantitative analyses to reassess the species discrimination; (3) to deduce the best way to discriminate among different species: morphological characteristics, quantitative morphometric analyses, or a combined result of both; and (4) to examine the validity of the transfer of the species *twiggsensis* to the genus *Tethylamna* Cappetta and Case [21].

2. Geologic Setting

Farag and Ismail [6] proposed the term Observatory Formation for the white marly and chalky limestones exposed in the Observatory Plateau, north Eastern Desert, Egypt (Fig.1). The Observatory Formation was subdivided into four members; Lower Building Stone, Gizehensis, Upper Building Stone, and Guishi members. It is composed

mainly of white thickly-bedded chalky and marly nodular limestones, grading into white hard fossiliferous limestones, and intercalated in the middle parts with sandstone and dolomite beds [3].

The Observatory Formation is commonly rich in large benthic foraminifera such as *Nummulites* aff *pulchellus* (Hantken), *N. beaumonti* d'Archiac and Haime, *N. thalmanni* (Schaub), *Pseudolacazina schwagerinoides* (Blanckenhorn), *Idalina cuvillieri* Bignot and Strougo, *Rhabdorites minima* (Henson), and *Dictyoconus egyptiensis* (Chapman) [3, 11]. The Observatory Formation was assigned to the Lutetian according to its stratigraphic position [6]. However, a Bartonian age was proposed based on the large benthic foraminifera [5, 11, 12, 13, 28, 29].

In Wadi Garawi area, Observatory Formation is only represented by the Guishi Member, measuring about 67 m in thickness. The Guishi Member consists mainly of intercalations of grayish white limestones with yellowish fossiliferous marls, and some white, fine- to medium-grained sandstone horizons, rich in shark teeth (Fig.2).

3. Background of the genus Brachycarcharias

The genus *Brachycarcharias* Cappetta and Nolf [17] is a Paleogene odontaspidid shark, inhabiting tropical shallow to deep waters, and is considered as an opportunistic top predator with various feeding and habitat preferences [17, 19, 20, 30, 31, 32]. The feeding and habitat preferences of *Brachycarcharias* may show some similarities with the present-day lamnid sharks, particularly *Lamna nasus* [33], mostly as a result of the apparently similar tooth morphologies [34].

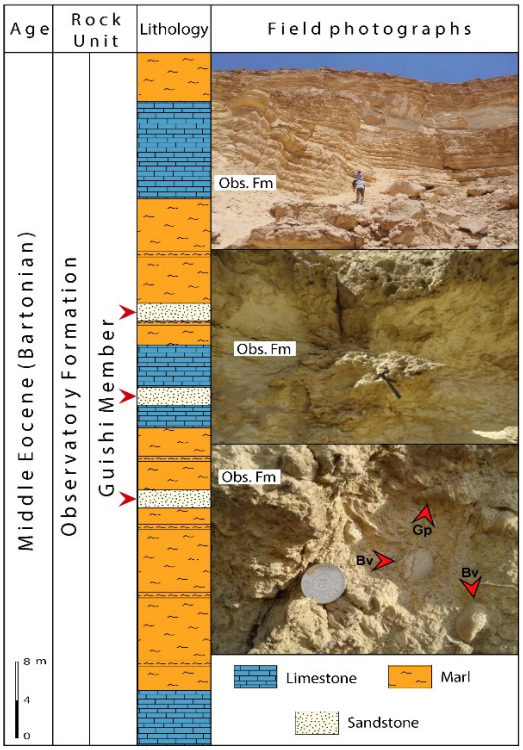

Fig.2. Lithostratigraphic section and field photographs of the Middle Eocene Observatory Formation Guishi Member) at Wadi Garawi, north Eastern Desert, Egypt (The studied *Brachycarcharias* species collected from the sandstone horizons indicated by the arrows). (a) General view of Observatory Formation (Guishi Member). (b) Chalky limestone in the Guishi Member. (c) Close view of Guishi Member, showing bivalves (Bv) and gastropods (Gp).

Brachycarcharias had a worldwide distribution in the Late Paleocene to the Late Eocene marine deposits of Pakistan, Georgia, Romania, Jordan, Japan, North America, and North Africa [19, 20, 35, 36, 37, 38]. In Egypt, *Brachycarcharias* was recorded from the Middle-Late Eocene deposits of Fayum area [39, 40, 41].

4. Materials and methods

A stratigraphic section of the Middle Eocene Guishi Member (Observatory Formation) at Wadi Garawi area, north Eastern Desert, Egypt (latitude 29° 47' N and longitude 31° 25' E) was compiled, measured and investigated in detail (Figs.1, 2). Fifty-eight well-preserved odontaspidid shark teeth specimens, belonging to the genus *Brachycarcharias* were collected from the loose sandstone horizons within the Guishi Member. The identification of the different *Brachycarcharias* species and the morphological terminologies in the present study largely follow the classification scheme of Welton and Farish [42] and that of Cappetta [15]. The landmarks that would illustrate the best morphological parameters were selected to be used to distinguish between the studied *Brachycarcharias* species. All the materials are deposited in the Geological Museum, Helwan University, Egypt.

The collected *Brachycarcharias* teeth specimens were sorted and identified to the species level according to the distinct morphological features characterizing the crown and root. The examined morphological features include the internal mesial cutting edge, internal distal cutting edge, main cusp, lateral cusplets, lingual crown ornamentation, root lobes and overall size [43]. Morphometric analyses on well-preserved teeth were carried out to exhibit the morphological variations among the qualitatively-discriminated *Brachycarcharias* species.

Such analyses include digitizing eleven two-dimensional landmark coordinate points on specific locations on the tooth using ImageJ software (Fig.3) [23, 27, 44]. The landmarks selected for the present study were defined based on their position on the tooth (1, cusp apex; 2, 8, junction of cusplet edge and root; 3, 7, lateral cusplet apices; 4, 6, junction of cusp and lateral cusplet edges; 5, center of the inner edge of the root; 9, 11, apex of root lobe; 10, maximum curvature of root center) (Fig.3).

A generalized procrustes analysis (GPA) [47] was performed using the MorphoJ software package on the landmark coordinates[48]. Removal of differences in location of landmarks is achieved by centering

configurations (i.e. the landmarked tooth). This involves calculating the centroid of each configuration [49], and then making the centroid the origin of a new coordinate system. GPA aims to remove size effects by rotating, translating, and scaling the landmarks to maintain their geometric relationships. All the configurations were rescaled to share a common centroid and exclude the differences in size. Removal of differences in orientation between two configurations is achieved by rotating one configuration (the target form) around its centroid until it shows minimal offset in location of its landmarks relative to the other configuration (the reference form) [49]. A principal component analysis (PCA) was then performed to illustrate the morphological variations among the different *Brachycarcharias* species along the major principal axes (PC1 and PC2) [50]. In addition, thin plate spline deformation plots were used in order to visualize and compare the mean morphological shapes of the *Brachycarcharias* species [51].

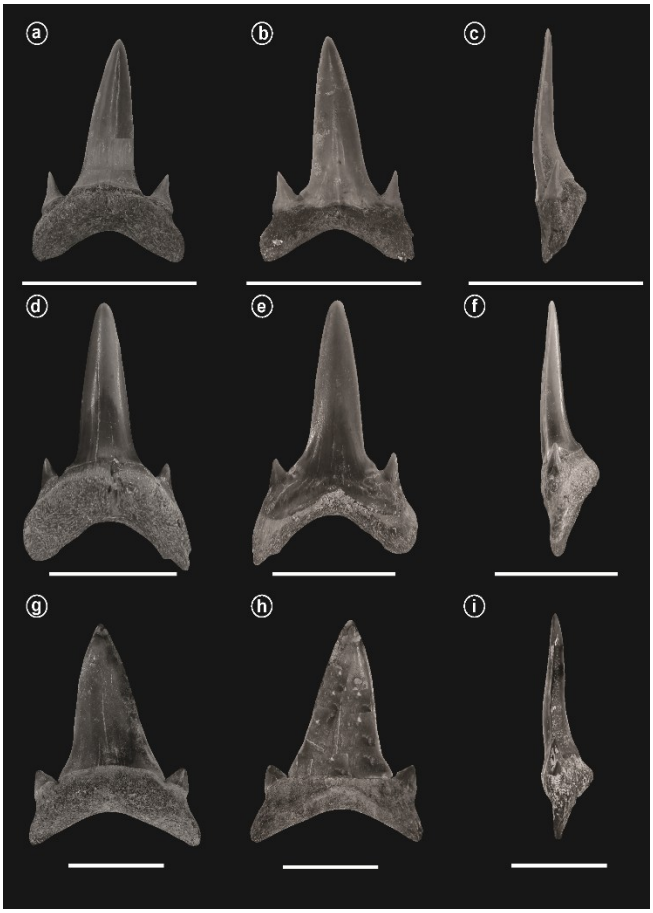

Fig.3. Representative fossil teeth of *Brachycarcharias* analyzed in this study. (a-c) *B. atlasi* [45], GST 2943; (a) lingual view, (b) labial view, and (c) mesial view. (d-f) *B. lerichei* [46], GST 2915; (d) lingual view, (e) labial view, and (f) mesial view. (g-i) *B. twiggsensis* [22], GST 2875; (g) lingual view, (h) labial view, and (i) mesial view. Scale bars = 1 cm.

5. Results

5.1. Qualitative study

The *Brachycarcharias* specimens were assigned to three different species based on their qualitative characteristics (Fig. 3). The recognized species are *Brachycarcharias atlasi* [45] (31 specimens), *B. lerichei* [46] (9 specimens), and *B. twiggsensis* [22] (18 specimens). Variations in the crown and root morphology were used to discriminate among the *Brachycarcharias* species. Nevertheless, all the recognized *Brachycarcharias* species have some similar characters, including a triangular main cusp; sharp, biconvex cutting edges; sharply-pointed, medially-curved lateral cusplets; cusplets strongly convex lingually; bilobate root, with wide, U-shaped interlobe area; and elongated, divergent root lobes, with rounded ends.

Brachycarcharias atlasi [45] is distinguished from *B. lerichei* [46] by having more distinct lingual ornamentation on the main cusp and the lateral cusplets, mesiodistally-narrower, less triangular lateral cusplets, and a more labiolingually compressed root. *B. atlasi* [45] also differs from *B. twiggsensis* [22] by being smaller in overall size, having lingual crown ornamentation, and a mesiodistally-narrower main cusp. *B. lerichei* [46] teeth exhibit smaller overall size and narrower main cusp than those of *B. twiggsensis* [22]. In addition, the teeth of *B. lerichei* [46] are characterized by a single pair of lateral cusplets while those of *B. twiggsensis* [22] may develop a second pair of cusplets.

5.2. Quantitative study

The generalized Procrustes analysis was utilized to provide average shapes of the studied *Brachycarcharias* species (Table.1). Only the first two (PC1 and PC2) of the five axes produced by the principal component analysis for the different species of *Brachycarcharias* explain more than 99% of the total morphological variation (Table.2). The principal component analysis exhibits some morphological overlap between *Brachycarcharias atlasi* [45] and *B. lerichei* [46]. However, a prominent morphological difference between these two species and *B. twiggsensis* [22] is illustrated (Fig.4).

Table.1. 2D-landmark coordinate data for the average shape of the studied *Brachycarcharias* teeth using GPA (Generalised Procrustes Analysis).

Landmark	Axis (x)	Axis (y)
1	0.19744974	-0.56191461
2	0.22145042	0.14658627
3	0.24560555	0.02411472
4	0.16206793	0.06391617
5	0.01018834	-0.04316467
6	-0.16583293	-0.06027277
7	-0.20205245	-0.14956500
8	-0.25961377	-0.04566987
9	0.17704094	0.36127979
10	-0.04136363	0.12489695
11	-0.34494013	0.13979301

Table.2. Variance explained by principal components of the interspecific analysis of *Brachycarcharias*.

Principal component	Eigenvalues	Variance %	Cumulative %
1	0.01040755	90.97	90.97
2	0.00098185	8.582	99.552
3	0.00002420	0.212	99.764
4	0.00001902	0.166	99.93
5	0.00000799	0.07	100

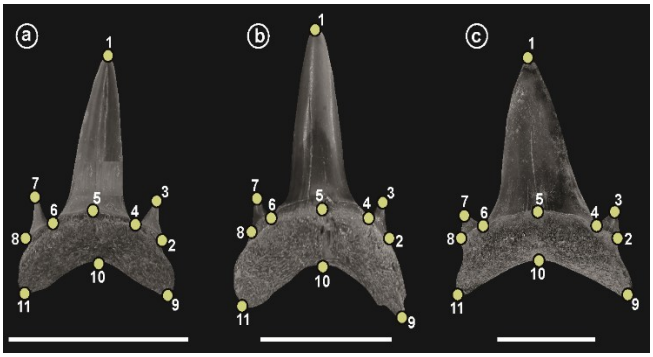

Fig.4. Location of landmarks for geometric morphometric analysis on (a) *B. atlasi*, GST 2943, (b) *B. lerichei*, GST 2915, and (c) *B. twiggsensis*, GST 2875. (1, cusp apex; 2, 8, junction of cusplet edge and root; 3, 7, lateral cusplet apices; 4, 6, junction of cusp and lateral cusplet edges; 5, center of the inner edge of the root; 9, 11, apex of root lobe; 10, maximum curvature of root center). Scale bars = 1 cm.

The mean morphological shapes of the different *Brachycarcharias* species are visualized through thin plate spline deformation plots (Fig.5). Shape variations are illustrated through the length of the internal mesial and distal cutting edges, height of the main cusp, lateral cusplets, and root, and the width of the main cusp, lateral cusplets, and root (Fig.5).

The internal mesial and distal cutting edges of *Brachycarcharias lerichei* are larger than those of *B. atlasi* and shorter than those of *B. twiggsensis*. *B. twiggsensis* shows higher main cusp and lateral cusplets than *B. lerichei* and *B. atlasi*, respectively. The root of *B. atlasi* is more compressed than that of *B. lerichei* and *B. twiggsensis*, respectively (Fig.5). The main cusp, the lateral cusplets, and the root are wider in *B. twiggsensis* than in *B. atlasi* and *B. lerichei* (Fig.5).

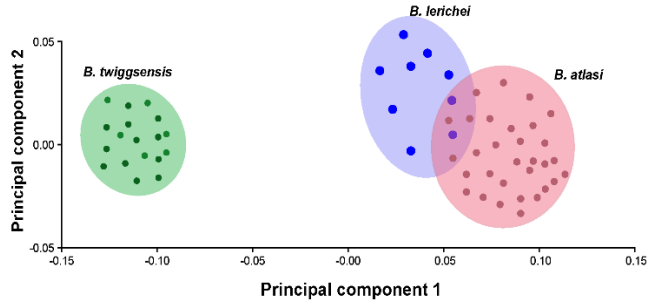

Fig.5. A scatter plot of principal component scores (PC1 vs PC2) of *Brachycarcharias atlasi*, *B. lerichei*, and *B. twiggsensis*.

6. Discussion

The shark *Brachycarcharias* Cappetta and Nolf [17]is represented in the Guishi Member of Observatory Formation by isolated teeth, assigned to three different species: *B. atlasi* [45], *B. lerichei* [46], and *B. twiggsensis* [22]. *Brachycarcharias atlasi* [46] appears to be restricted to the Thanetian-Ypresian of North America and North Africa (Morocco and Tunisia) [18, 20, 37, 45] .

B. lerichei (46) is the oldest species of the genus. It reached the most extensive distribution in the Tethys realm and North America during the Ypresian [17, 18; 20, 32, 37, 45, 52, 53, 54, 55] , and extended to the Priabonian of Japan [56]. *B. twiggsensis* [22] was recorded from the Ypresian to Priabonian in different regions of the world, e.g., USA, Uzbekistan, Pakistan, Georgia, Romania, Jordan, Morocco, and Fayum area in Egypt [20, 35, 36, 38, 41, 57, 58, 59].
The distinction among these species is confirmed through the qualitative characteristics and through the quantitative morphometric analyses as well. Morphometric analyses maintain the geometry of landmark configurations, and therefore transforms the actual shapes into statistical results [23, 26, 27]. The generalized Procrustes analysis helps to isolate the size, position, and orientation of the landmarks [60]. These analyses show a great significance in discriminating the three recognized species.

The morphological characteristics used in the present work to identify the *Brachycarcharias* specimens include internal mesial cutting edge, internal distal cutting edge, main cusp, lateral cusplets, and root lobes (Fig. 3). The studied *Brachycarcharias* species share some morphological features (e.g., a triangular main cusp; sharp, biconvex cutting edges; sharply-pointed, medially-curved lateral cusplets; strongly-convex cusplets lingually; bilobate root; U-shaped interlobe area; elongated, divergent root lobes). However, they can be differentiated based on some other features (e.g., tooth overall size; number of cusplet pairs; width of main cusp and cusplets) (Fig. 3). *B. twiggsensis* [22] show the largest overall size, the widest crown base and lateral cusplets. *B. atlasi* (45) and *B. twiggsensis* [22] have up to two pairs of lateral cusplets while *B. lerichei* [46]bears only a single pair. The lingual crown ornamentation of *B. atlasi* [45] is absent in *B. lerichei* [46]and *B. twiggsensis* [22]. *B. atlasi* [45] has a more labiolingually compressed root (Fig. 3).

In addition to the differences in the morphological characteristics, the quantitative analyses, including principal component analysis and deformation plots, show significant variations among the different *Brachycarcharias* species (Fig. 4-6). Principal component analysis shows that *B. twiggsensis* is well separated from *B. lerichei* and *B. atlasi*. The length of the internal mesial and distal cutting edges, height of the main cusp, lateral cusplets, and root, and the width of the main cusp, lateral cusplets, and root vary among *Brachycarcharias* species. They are the largest in *B. twiggsensis* [22], and the smallest in *B. atlasi* [45] (Fig. 6). All these quantitative results support a species-level discrimination among the qualitatively distinguished

Brachycarcharias species. It can be concluded that the qualitative examination combined with the quantitative morphometric analyses provide a better species-level discrimination of *Brachycarcharias* species.

The significant variation between *B. twiggsensis* [22] and the other *Brachycarcharias* species, *B. lerichei* [46]and *B. atlasi* [45], supports the reassignment of the species *B. twiggsensis* to a different genus, *Tethylamna*, as proposed by Cappetta and Case [21]. Anterior teeth of *Tethylamna* Cappetta and Case [21], recovered from the Lutetian of Alabama, exhibit a broader cusp with less convex lingual face than those of *Brachycarcharias* Cappetta and Nolf [17], and hook-like, lingually-inclined cusplets.

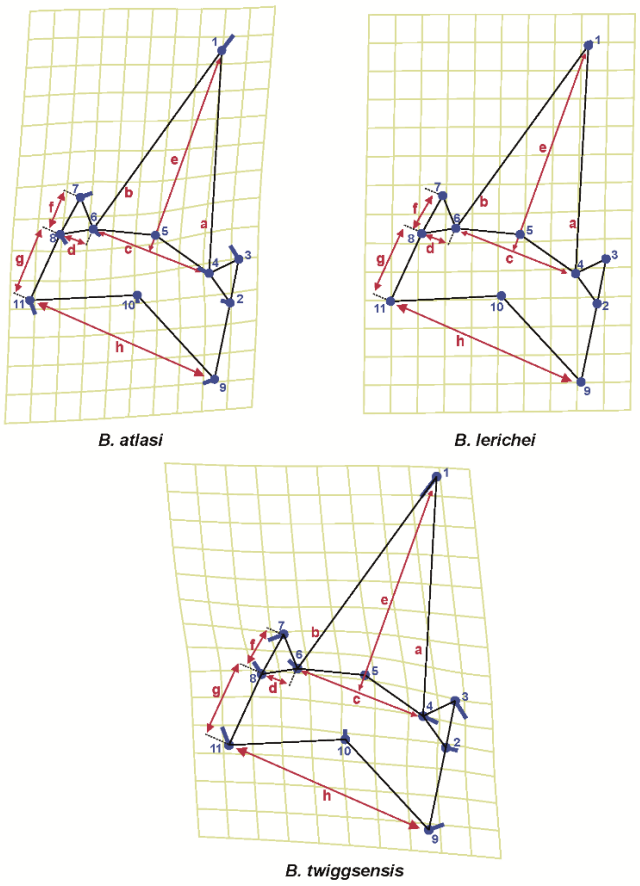

Fig.6. Thin-plate spline deformation plots for the mean morphological shapes of *Brachycarcharias atlasi*, *B. lerichei*, and *B. twiggsensis*. (a: internal mesial cutting-edge length (cusp only), b: internal distal cutting-edge length (cusp only), c: width of main cusp, d: width of lateral cusplets, e: height of main cusp, f: height of lateral cusplets, g: root height, h: root width)

Conclusion

(1) The Middle Eocene deposits at Wadi Garawi area, north Eastern Desert, Egypt, is represented by the Guishi Member of the Observatory Formation, comprising a distinct limestone-marl succession with some sandstone horizons, from which the studied shark teeth were collected.

(2) The fifty-eight teeth specimens collected from Guishi Member were attributed to three different species of the genus *Brachycarcharias*, based on their morphological features. These are *B. atlasi* [45], *B. lerichei* [46], and *B. twiggsensis* [22].

(3) The qualitative discrimination among the *Brachycarcharias* species was reassessed through quantitative morphometric analyses. These morphometric analyses include configuration of landmarks, generalized procrustes analysis, principal component analysis, and thin-plate spline deformation plots. Such analyses illustrated considerable variations in the length of the internal mesial and distal cutting edges, height of the main cusp, lateral cusplets, and root, and the width of the main cusp, lateral cusplets, and root.

(4) The qualitative examination, along with the quantitative morphometric analyses introduce an excellent species-level discrimination method for the *Brachycarcharias* species. These analyses also confirm the reassignment of *B. twiggsensis* to the genus *Tethylamna* Cappetta and Case [21].

Disclosure Statement

No potential conflict of interest was reported by the authors.

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