Review

Human Dento-Facial Evolution: Cranial Capacity, Facial Expression, Language, Oral Complications and Diseases

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Abstract: Objectives: To review dento-facial evolution based on fossil data, comparative anatomy, developmental biology and genetics. Modern human evolution reveals profound insight into the technical and biological challenges faced by clinicians in daily practice of dentistry. Materials and Methods: An analysis and review of the literature is presented to further explain the evolutionary forces that have shaped hominins. Results: Modern human evolutionary morphological and biological adaptations allowed improvement of cognitive ability, facial expression, smile and language. However, the increased cranial capacity correlates inversely with a decrease in size of the maxillary and mandibular bones, weakening of the muscles and facial shortening, contributing to dento-facial complications. Moreover, the distinctive differences in origin and development of the dento-facial components have further contributed to these maladies. In addition, human lifestyle transition from nomadic to sedentary increased the incidence of oral diseases. Conclusions: Knowledge of human evolutionary patterns can improve the quality of response by clinicians to biological challenges. The limitations in current treatment modalities can be explained, in part, due to the complexity of the life forms that resulted from evolution. Although there are no rules to predict how evolutionary forces will shape modern humans, the evolution of the dento-facial complex reveals profound insight into our connection to other forms of life and nature.

Keywords: evolution; maxillary evolution; mandibular evolution; phonetics; language; facial evolution; facial recognition; smile

1. Introduction

The origins of life on Earth remain unknown, but certainly living organisms have proliferated, diversified, adapted and evolved to complex organisms. Currently, the oldest evidence of life on Earth dates back to 3.9 Ga (gig years) ago according to the graphite where biogenic substances were discovered [1]. Since life initiated, billions of years of evolutionary processes have fashioned the species as we know them, including modern humans. Homo sapiens (modern humans) belong to the family of Hominins along with other members from the genera Homo, Australopithecus, Paranthropus and Ardipithecus [2]. The human-like traits that appeared in the hominin lineage are bipedalism and blunt canine teeth. A relative recent feature seen in late hominins is an increase in the cranial capacity. The cranial capacity expanded from 350 cc (Sahelanthropus tchadensis, Ardipithecus ramidus) to 1500 cc in modern humans [3].

The increased cranial capacity correlates inversely with a decrease in size of the maxillary and mandibular bones, weakening of the muscles and facial shortening. These series of events, evidenced during the last 7 million years, have contributed to dento-facial complications [4]. Moreover, human lifestyle transition from nomadic to sedentary increased the incidence of oral diseases about 12,000 years ago. However, positive products of the morphological changes have been the smile, facial expression, language, cognition and more human abilities [5,6].
Regardless of how life originated, life forms and the modern human evolution reveals profound insight into the biological challenges faced by clinicians in daily practice. An analysis and review of the literature is presented to further explain the evolutionary forces that have shaped hominins based on fossil data, comparative anatomy, developmental biology and genetics.

2. Hominins and the Genus *Homo*

Hominin is one of the branches of the Hominoid tree. Hominoids (Apes) are characterized by the orthograde posture, broad pelvis, wide chest, stiff lumbar spine, and lack of a tail. Although the hominoid fossil record is incomplete, the appearance is estimated to be between 25 to 34 mya (million years ago). The oldest hominins known are *Sahelanthropus tchadensis* and *Orrorin tugenensis* from between 6 to 7 mya. A descendant, the *Australopithecus*, appeared about 4 mya; they were terrestrial bipeds that lived in trees for protection. *Australopithecus*, a successful branch of the hominin lineage, persisted for about three million years until it went extinct about 1.5 mya [2].

The genus *Homo* lacked the forelimb adaptation needed for climbing, marking a transition in the locomotor system and posture favoring bipedalism [7,8]. *Homo habilis*, the oldest member of the genus *Homo*, dated to 2.3 mya, is associated with tool making, the first ever known discovered in Ethiopia [9]. A later *homo*, *Homo erectus*, seemed to be more capable of adapting to different ecosystems, probably due to their cognitive capacity (1250 cc). Approximately 2 mya *H. erectus* became the first hominin to migrate out of Africa. Fossils of *H. erectus* can be found in Africa and Eurasia from 2 mya to 100 kya (thousand years ago) [2].

*Homo heidelbergensis* is known as “Archaic” *Homo sapiens* (modern humans). Very similar in cranial capacity, dento-facial anatomy and body proportions to modern humans, *H. heidelbergensis* appeared about 700 kya. A probable descendant of *H. heidelbergensis* is *Homo sapiens neanderthalensis*. *H. neanderthalensis*’ climate adaptations and encephalization along with strong physic allowed the species to succeed from 500 kya to at least 30 kya [10,11]. Contrary to the thought that some hominins species that preceded modern-humans went extinct, recent studies have evidenced portions of Neanderthal and/or Denisovan genome carried by non-African humans [12,13]. The evident phylogenic relationship between *H. sapiens* and *H. sapiens neanderthalensis* is undoubtedly a topic of interest to science, as any finding can shed light on the origin/definition of modern humans [13].

The emergence of modern humans is currently considered to be about 300 kya [14]. Modern humans’ ability to produce sophisticated tools, climate adaptation and complex behavior (hunting, language, trade) has been associated with the increased cranial capacity (1500 cc). Over 7 million years of evolutionary processes have shaped modern humans to their current form. The anatomical features of modern humans were imperative for success as a species, but contributed to dento-facial changes that challenge the daily clinical practice of medicine and dentistry.

3. Cranial Capacity/Cognition

Although hominins cranial capacity has expanded over the last 4 million years, one of the major periods of brain growth has been identified during the appearance of the genus *Homo* about 2.5 mya, when the brain size in *H. habilis* increased to an average of 640 cc and to 1250 cc in *H. erectus*. The second major period is coincident with the appearance of the *H. sapiens*, the cranial capacity of which averaged 1450 cc. [3].

Encephalization has been associated with changes in quality of diet (fire/cooking), as suggested by the expensive-tissue hypothesis. Stone tools and fire/cooking may have facilitated the ingestion of rich in calorie nutrients that allowed the brain to grow [15]. Stone tools are associated to *H. habilis*. It is known that early species like Neandertals and *H. heidelbergensis* had learned to control fire [15]. Albeit, early specimens of the genus *Homo* have similar cranial capacity to *Australopithecus*, a change of diet is noticed in their teeth.
reflecting a less hard/abrasive diet. A soft diet was allowed by the invention of stone toolmaking and fire/cooking mastery.

Other theories associated the climate variances with human encephalization. The variability selection hypothesis basically refers to how individuals were forced to move into novel habitats, altering the use of resources due to the extreme fluctuations in the environment. As well as how the extreme climates changes caused abrupt and environmental shifts playing pivotal roles in major adaptations that led to \textit{H. sapiens} [16].

Most likely, human encephalization was favored by a combination of several factors over time, rather than a unique cause. Factors like fire/cooking, complex social activities, climate, and predation among others. Without a doubt, human cognitive abilities have transformed every aspect of our lives.

4. Teeth

The teeth are considered to be one of the major evolutionary innovations in nature. The first evidence of tooth-like structures was identified in conodonts species, dating back to approximately 520 million years ago [17,18]. Hypotheses have been suggested to explain whether teeth evolved from external denticles or independently. The inside-out hypothesis suggests that dermal denticles and teeth evolved de novo independently. The foundation of the inside-out hypothesis is the embryogenic differences in development from external (dermal denticles) and internal denticles (teeth). However, this principle was found to be inaccurate, and recent studies have demonstrated that teeth can develop from dermal, endodermal or mixed epithelia. The inside-out hypothesis has been undermined substantially. In contrast, the outside-in hypothesis proposes that external tooth-structures and teeth (internal odontodes) share a common origin. The outside-in hypothesis suggests that teeth emerged through odontogenic competence from external dermis to internal dermis. Collected evidence has positioned the outside-in hypothesis as the most compelling explanation for the origin of teeth. Although in living species the development of internal and external odontodes are distinctive, the distinction may have not appeared until the evolution of jawed-vertebrates [18].

The origin of teeth is still a topic of debate. However, the complex developmental biology and genetic interactions underlymg tooth formation (enamel, dentin, periodontium) are currently better understood. Since tooth structures emergence, they have evolved among species for a variety purposes [19,20].

Teeth in dolphins help to enhance sonar ability used for echolocation and navigation [21]. Shark denticles decrease drag and turbulence enabling faster and quiet swimming for preying, but more interestingly, shark denticles can sense changes in electrical currents, further enhancing preying capabilities by detecting electromagnetic fields of living organisms [22]. Narwhals used their teeth to sense chemical changes in water for locating food sources, hunting and intersexual selection [21]. Snails have about 1000 to 20,000 teeth that they use for scraping and feeding. Snails have evolved to eat everything, making them herbivores, carnivorous, omnivorous and detritivorous [22].

Human teeth physiology evolved for mastication, language, phonetics and esthetics. In medical and dental fields as the acceptable esthetic demands from patients increase, in dentistry particularly, the origin of teeth and the maxillary/mandibular complex is of great importance to understand the value of the unit.

5. Maxilla and Mandible

Jaws were crucial for the success of different species, including humans. The maxillary/mandibular complex may have developed about 480 million years ago. However, the oldest evidence of jawed species is detected in Placoderms that lived in the Silurian period about 440 mya [23]. Recently, fossils from \textit{Entelognathus} provided evidence linking extinct placoderms to living bony fishes. \textit{Entelognathus} possessed dentary jaws and interestingly an upper jaw composed of pre-maxilla and maxilla. The finding connects extinct jawed
species to living jawed species, revealing information about the evolution of a complex maxilla that ultimately led to the complex human maxilla and mandible [24].

About 225 million years ago a novel temporo-mandibular joint (TMJ) formed [25]. The novel TMJ was connected to the three-ossicle ear and the shortening of the mandible. Through the breakdown of Meckel’s cartilage, independently multiple mammalian lineages evolved a definitive middle ear. The formation of the three ossicles and jaws is distinctive of mammals, unlike reptiles and birds that have only one middle ear ossicle [25]. The three ossicles transferred enhanced hearing in the fluid and membranes of the inner ear.

The innovation of jaws allowed species diversification. Commonly used to catch prey, different forms of jaws can be found in several species like ants and spiders. Especially in humans, more evolutionary processes that led to the origin of the complex unit formed by teeth and maxillary/mandibular bones are yet to be unveiled. A product of this union yielded what we have named “Periodontium” in modern humans. Dental and oral medicine is dedicated to the treatment, study, diagnosis and prevention of oral diseases. Knowledge about the origin of the dento-facial complex is imperative in current dentistry for clinicians to diagnose and develop efficacious therapies.

6. Periodontium

The masticatory mechanism of teeth is locationally and functionally associated with the jaws. The tissues involve interacted in humans (mammals) to develop a periodontium. The periodontium as dentistry defines it in humans appeared 270–290 million years ago in stem mammals. Dimetrodons of the Permian period are one of the first species possessing all the tissues of the human periodontium [26]. The periodontium comprises bone, cementum and periodontal ligament. The physiological role of these tissues includes tooth eruption, anchorage, force absorption and provides proprioception information. Molecular and cellular mechanisms that maintain homeostasis, integrity, architecture and communication between the tissues of the periodontium have yet to be decoded [27].

Nonetheless, practitioners in dentistry have evidenced the impact by disease of the disruption of any of the tissues in the periodontium. Disturbances in the periodontium can result in long junctional epithelium, bone loss, ankyloses, and tooth loss. Moreover, disturbances may impact esthetics, a crucial factor influencing dentistry, which is undeniably of interest to clinicians and patients. With the increase of dental implants popularity to treat edentulous spaces resulting from tooth loss, clinicians are constantly challenged to provide functional and esthetic outcomes [28]. Preservation or restoration of the soft and hard tissue architecture provided by the dento-periodontium following tooth loss is a regular clinical scenario in the practice of dentistry [29]. However, consistency of results, reliability of treatment modalities and long-term prognoses have been limited [28–30]. The anatomy and architectural structures formed by the teeth, bones and periodontium have billions of years of evolution behind them that clinicians must understand. Limitations of the treatment modalities can be explained, in part, due to the sophistication of the tissues and lack of knowledge on the origin and cell behavior as a unit. Nowadays, as implant dentistry complications increase, researches are providing evidence about the importance of tooth preservation and with it: the periodontium. Research has shown that tissues formed around dental implants are more susceptible to bacterial challenge than the periodontium formed around teeth. Furthermore, comprehension of the biological and evolutionary complexity of the periodontium would create a more objective clinical practice.

7. Human Facial Expression, Language and More Human Abilities

The human smile is a unique facial expression, the origin of which is an open inquiry among species and in human evolution.

The smile is expressed on the face by the combined relaxation/contraction of the different muscles involved (e.g., zygomaticus major and minor, orbicularis oculi, etc.), depending on the type of emotion that the person is expressing, and also differs from person to person as the smile patterns of each person are completely different. The functions of the
smile are signaling and emotion expression, crucial for human language [31]. The nature of the human smile is versatile, having been associated with multiple social tasks including love, sympathy, laughter and war [32]. Smile signaling/function may differ in other species, since it is not unique to humans. For example, in some non-human primates, the smile may be a sign of submission, threat and warning [31]. From a medical perspective, the smile has a direct impact on cosmetic surgery and dentistry. Alterations, developmental and/or acquired, in the smile–teeth–gingiva relationship and as part of the facial framework could modify patient esthetics, affecting clinical outcomes and ultimately social interactions [33]. Current medical/dental standards are aware of the significance of the smile as part of a successful treatment outcome.

Language enabled humans to develop, speak and communicate as a species. Modern human language is composed of gestures and speech. Gestural language may have emerged to enable cultural transmissions of stone tool-making skills in early hominins. While speech may have coevolved as a result of more complex hominins interactions (e.g., social, trade) in ancestors of Homo sapiens neanderthalensis and Homo sapiens during the Middle Pleistocene [6]. Archeological and genetic evidence show that Homo sapiens neanderthalensis an extinct species of archaic humans, possessed some form of language unlike Homo erectus. A language requires muscle flexibility that was, in part, allowed by muscle relaxation during cranial growth. In contrast to powerful masticatory muscles evidenced in most primates, masticatory muscles are considerably weaker and smaller in both modern and fossil members of Homo. Human soft diet and ability to speak do not require strong musculoskeletal structure, nor powerful teeth.

Anthropology recognizes the importance of facial expression and language for human relationships, society and culture. Individual facial recognition requires phenotypic diversity and variation. The number of muscles in the face, larynx and forearm in modern humans is greater when compared to other mammals [34]. The findings are in accordance with the muscle complexity that would be required for language (vocal communication) and to smile (facial expression). The human chin has no functional importance, but is a unique feature used to define Homo sapiens [35]. Absent in archaic humans, the development of the human chin that emerged at a time of mid-facial reduction and mandibular shortening contributes significantly to individual facial recognition [36].

Therefore, human cognitive ability can be explained, in part, as the response to the increase in complexity of hominins social interactions. Nevertheless, complex social interactions are not only reflected by human encephalization [15]. Successful social interactions are highly influence by gestural expression allowed by the cranio-facial musculature evolution [34]. Albeit genetic and epigenetic events have enhanced human facial expression, individual recognition and linguistic capabilities over the last 500,000 years, dento-facial complications have increased.

8. Oral Diseases and Dento-Facial Complications

Human evolution is replete with achievements such as the invention of tools, writing, scientific method, mastering of fire/cooking, agriculture and others that all together have influenced human culture. Modern human lifestyle was drastically changed about 12,000 ya, when humans transitioned from a nomadic to a sedentary life. Such a transition has not only impacted human’s health, but also the Earth and other species around us [36]. The major leap forward allowed by agriculture has been associated with the increase of dental caries and periodontal diseases, the current two main causes of human tooth loss in modern society.

Association of corn-based agriculture with an increase of caries lesions has been reported [37–41]. Products rich in carbohydrates (sucrose and starches) of domesticated plants with agriculture, combined with food preparation sophistication, have contributed to dental caries. Furthermore, tooth microwear produced by the diverse consistency of aliments create areas for bacteria and micro food particles accumulation [42]. Contrary
to the coarse alimentation of prehistoric humans, modern human soft diet, bacteria and microwear may have promoted caries initiation and progression.

The decline in modern human’s oral health was also affected by periodontal disease occurrence. Beyond oral health, periodontal disease has impacted humans’ social interactions, impacting self-esteem in affected patients. Patterns of dimension reduction of the face, jaws and teeth have been observed in archeological evidence from Neolithic humans [37,39]. This correlates with the increase of periodontal disease incidence [42,43]. The cranio-facial evolution has contributed to dento-facial changes, including an increase in the incidence of impacted teeth and overcrowding in modern humans. Overcrowding creates areas for plaque accumulation and calculus formation, increasing the risk of periodontal disease [44,45]. These human features are associated with periodontal disease progression and prevalence, which contributes to elevated levels of morbidity in our species [40,41,44,45].

Human evolution favored cranial growth by reducing the dimensions of the maxillary and mandibular bones that left limited space for tooth eruption. As a result, the incidence of malocclusion, impaction and overcrowding increased [4,44,45]. Teeth and maxillary/mandibular bones did not reduce dimensions proportionally, mainly due to the differences in origin and development [4,17,18]. General patterns of dental morphological evolution include the loss of the diastema, present in archaic humans. The prevalence and pattern of impacted teeth seem to be similar among different populations [46–48]. Despite a change in diet to a less hard/abrasive alimentation, the eventual absence of third molar formation has not been associated with an evolutionary anatomical adaptation [49,50]. The distinctive differences in origin and development of the teeth, maxillary/mandibular bones, cranio-facial bones and musculature have contributed to dento-facial complications such as an increase in the incidence of malocclusion, impaction, overcrowding teeth and obstructive sleep apnea.

Another negative side effect has been the pharyngeal collapse, posterior displacement of the tongue into the pharynx and shortening of the mandible that together have contributed to obstructive sleep apnea [51]. The oropharyngeal evolution is connected to bipedal posture and brain volume increase. Bipedal specializations are evidenced in Australopithecus fossils from 4.2–3.9 million years ago [52]. Bipedalism evolved well before the large human brain and required a smaller oral cavity for the arrangement of the center of gravity of human cranium. The upper airway evolution along with the facial shortening facilitated the phonetic ability and the invention of human language.

In addition, cranio-facial growth is influenced by masticatory forces, which in part is altered by diet [44]. Thus, cranio-facial structures adapt to individual species’ needs. In particular to humans, the fire/cooking mastery and agriculture-related dietary modifications over time affected the mastication, decreasing humans’ need for strong musculature and teeth required for a hard abrasive alimentation. Stedman et al. provided evidence that the gene encoding the predominant myosin heavy chain (MYH) was inactivated by a mutation. The mutation appeared 2.4 million years ago as estimated by molecular clock, predating the appearance of the modern human body size [31]. The chewing activity of humans is less efficient when compared to other mammals and archaic hominins. Loss of this protein isoform may have been associated with a marked size reductions in entire masticatory muscle fibers that also favored cranial capacity increase by muscle relaxation. Overall, the modern human experienced morphological changes driven by evolutionary processes that negatively impacted health. However, the morphological adaptations presented an opportunity that ultimately allowed humans to improve cognitive ability, smile, speech, and individual facial recognition.

9. Perspectives

Dentistry has experienced periods of major excitement followed by severe disappointments. The limitations in the treatment modalities can be explained, in part, due to the complexity of the life forms that resulted from evolution and dynamics between
bacteria, viruses, immune responses, genetic and epigenetics factors that have caused dento-facial complications.

Caries and periodontal disease remain the main pathologies affecting oral health causing tooth loss [53,54]. The standard of care for caries and periodontal disease remains primitive modalities consisting of the removal of the infected tissues. Treatment of caries, a disease mainly caused by Gram-positive bacteria, consists of mechanical removal of infected dentin and application of fillers (amalgam, composite, ionomer, gold or ceramic materials). Periodontal disease is caused by protective and destructive immune responses responding to bacterial and viral pathogens. Currently, the treatment for periodontal disease constitutes mechanical therapy (non-surgical and surgical), antiseptics and systemic antibiotics [54].

Sophisticated treatments like regeneration have yielded long-term disappointing results. Regeneration remains an important therapeutic goal in dentistry. However, the cellular inductive processes that regulate the differentiation and maturation of the teeth and periodontal tissues are not well understood yet. Considering the complexity of evolution and organogenesis in tooth development, it may be difficult to perceive that the mere placement of devices such as membranes, grafts (autologous, allografts, xenografts or synthetics) and growth factors would be sufficient to induce formation of the highly sophisticated periodontal tissues that resulted from billions of years of evolution. The case of guided tissue regeneration for periodontal patients is an example in dentistry of a period of major excitement followed rapidly by severe disappointment. Presently, “regenerative” procedures continue to be performed in hopes of an occasional dramatic result limited by current knowledge and technology [55].

Implant therapy for tooth replacement along with dental implant related surgeries that involve soft tissue and bone augmentation have increased significantly. Nevertheless, it has been demonstrated that peri-implant tissues are more susceptible to bacterial/viral challenges when compared to periodontal tissues (periodontium) [56]. Peri-implantitis is characterized by inflammation of the peri-implant tissues and loss of supporting bone. The human-made disease of peri-implantitis is considered to be growing problem in dentistry [57]. Perhaps, the differences in susceptibility lie in the differences in origins of the surrounding tissues. The periodontium forms from Hertwig’s epithelial root sheath, while the junctional epithelium from the reduced enamel epithelium [58,59]. The peri-implant tissues form as a response to the phenomena of osseointegration during the wound healing process, divided into bone and soft tissue compartments [56]. Developmentally, the formation of the periodontium when compared to peri-implant tissues is superiorly organized and sophisticated. Moreover, implant dental therapy limitations to restore the original architecture found in the natural pristine permanent dentition have been evidenced. However, dental implants have provided acceptable treatment outcomes that clinicians and patients have benefited from [30]. In the quest to provide functional and esthetics results, clinicians have suggested a variety of techniques, grafts and implant design modifications with occasionally disastrous results [28]. Currently, no treatment modality is able to restore the tissues that nature has developed during millions of years of evolution.

Treatment for impacted teeth consists usually of a combination of orthodontic and surgical treatment. Nowzari and Rodriguez, from an evolutionary perspective, reported on how tooth impaction in modern humans has compromised orthodontic treatments and recommended the use of a closed flap surgical technique for the management of impacted teeth [4]. Currently, the treatment of choice for obstructive sleeping apnea consists of devices for a continuous positive airway pressure (CPAP). Dentists and specialists seeking to prevent and/or provide reliable long-term results for treatment of these maladies are constantly challenged by inconsistent results. Authors have highlighted the importance of the evolutionary events that modern humans have experienced to understand in more depth current clinical challenges.
10. Conclusions

Human cognition capacity, language (gestural and speech) and capability of facial expression to smile are gifts of 3.9 billion years of evolution. Although there are no rules to predict how evolutionary forces will shape modern humans, knowledge of human evolutionary patterns can improve the quality of response to biological challenges. The evolution of the dento-facial complex reveals profound insight into our connection to other forms of life and nature.

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